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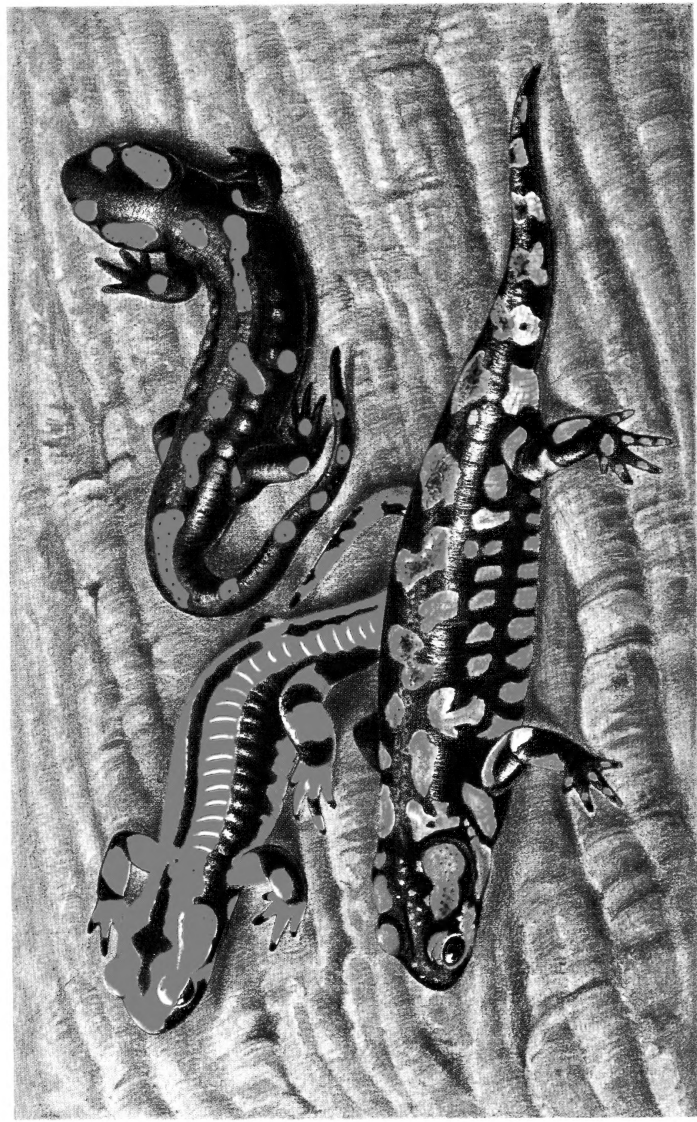
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THE
ANATOMY
OF THE
SALAMANDER





SALAMANDRA SALAMANDRA, L.



Var. Taeniata

Var. Molleri

Forma Typica

(After Boulenger, Proc. Zool. Soc. 1911.)

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THE ANATOMY OF THE SALAMANDER

BY
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B.SC. LOND., PH.D. READING

WITH AN
HISTORICAL INTRODUCTION BY
PROFESSOR F. J. COLE
D.SC., F.R.S.



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PREFACE

THE Salamander is well known to all students of Zoology as the animal most commonly dissected to exemplify the structure of the Amphibia Urodela. Notwithstanding its general use for teaching purposes, the accounts of the anatomy of this animal available in text-books are out of date, and even, in some respects, seriously misleading. It was with a view to closing this gap in our knowledge that the present work was undertaken. Its intention is to provide a general account of the anatomy and morphology of a tailed Amphibian—the Salamander, which shall, within limits, be comparable with the work of Ecker and Gaupp on its ecaudate relative—the Frog.

In the main the gross anatomy only has been dealt with, histology and embryology being excluded. The practical work has been carried out under a Zeiss binocular dissecting microscope, using magnifications of $\times 7.5$, and $\times 20$ for the finer details, supplemented by a microscopic examination of microtome sections where necessary. Any special methods used for the elucidation of particular systems, e.g. the lymphatic system, are dealt with in the text. All figures are original and have been specially drawn for this work by the author, with the following exceptions: Text-figures 1, 2, and 3 are taken from Willem (1923), Figs. 65, 66, and 67 have been redrawn (with Prof. Hoyer's kind permission) from Hoyer and Udziela, Fig. 53 is after Luther, and Fig. 82 has been modified from Bruner. I am further indebted to Mr. E. G. Boulenger and the Publication Committee of the Zoological Society of London for permission to reproduce the coloured plate appearing as the Frontispiece.

Although this work will probably make its greatest appeal to the teacher and advanced student, the requirements of the general student are provided for by means of summaries to the more specialized sections, and in the planning of the figures illustrating the more important systems, e.g. blood-vessels and cranial nerves. To meet the needs of the research worker and comparative anatomist an attempt has been made to collate as far as possible all the important literature dealing with each subject under review, and to give, whenever possible, tables of the synonyms used by previous authors, together with the dates and full details of the papers in question.

The Bibliography has been compiled with some care, and includes not only those publications which have direct reference to the subject-

matter of this work, but also papers dealing with the Histology, Embryology, and Physiology of the type, as well as a certain number of works, which, although not dealing specifically with *Salamandra*, have sufficiently important general bearings to justify their admission. This list does not pretend to be complete except in so far as the anatomy of *Salamandra* is concerned, and there must inevitably be many omissions. Nevertheless it is offered with the confidence that it will prove an adequate guide for any future investigation, either of *Salamandra* itself, or of any other closely related Urodele. In this connexion I must acknowledge with gratitude the invaluable assistance which has been freely given by the Librarian and staff of both the Zoological and General Libraries of the British Museum (Natural History), of the Science Library, South Kensington, the Library of the Royal College of Surgeons of England, and of the Royal and Zoological Societies. My importunate demands for books have always been met with courtesy, and expert advice in tracking down obscure references has been placed ungrudgingly at my disposal.

To my Tutor, Professor F. J. Cole, F.R.S., in whose laboratory the work has been done, my sincerest thanks are due. He is responsible not only for the original plan of the work, but also for stimulating its progress in times of doubt and difficulty. Moreover, he has closely associated himself with its publication by writing the Historical Introduction. I owe a debt of gratitude to Dr. N. B. Eales, whose constructive criticisms have helped to rectify many blemishes, for sharing with Professor Cole the arduous task of reading the proofs of this work. Their aid has been invaluable. I also desire to thank the numerous other Zoologists who have assisted in various ways. Among them I would name especially Dr. Chas. H. O'Donoghue, of Edinburgh University, who has offered valuable suggestions on problems connected with the vascular system, and Dr. F. H. Edgeworth, of Bristol, who has very kindly placed at my disposal his knowledge of muscle terminology—particularly in respect of the hyobranchial apparatus, and finally Professor H. Graham Cannon, of Manchester University, who has given very welcome technical advice with regard to the illustrations. I have also to acknowledge my indebtedness to the Council of the Royal Society and the Research Board of Reading University for generous grants, without which the publication of the work in its present form would not have been possible.

E. T. B. F.

THE UNIVERSITY, READING.

August 1933.

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HISTORICAL INTRODUCTION

IN a morphological treatise such as the present work it is only necessary to outline the history of the relevant anatomical and physiological literature. Therefore the numerous medieval legends which have condensed around the habits and medical importance of the Salamander, and the extensive literature relating to its alleged resistance to fire, will be disregarded. On this aspect of the subject the investigations of the learned Wurffbain (1683) may be consulted. A typical example of these fables was the belief that the asbestos fibre, the incombustible nature of which was soon recognized, was the hair of the Salamander, and it was sometimes even referred to as Salamander's wool.

There are several recognizable figures of *S. maculosa*, of varying degrees of excellence, in the earlier treatises on Natural History, such as Mattioli's *Commentary on Dioscorides*, Gesner, Paré, Imperato, Aldrovandus, Perrault, Seba, Owen, and Roesel, of which that of the last-named naturalist hardly exhibits the accuracy of so careful an observer of nature. Of the Amphibia the Frog and Newt were investigated before the Salamander, and much more thoroughly. The earlier workers, however, included a number of species under the term Salamandra, and considered themselves at liberty to expound the anatomy of any one of them without further discrimination. Hence for example Triton would be dissected and described as Salamander, as if the species were anatomically interchangeable. This introduces a difficulty of some importance in the interpretation of the older literature, and especially in those cases where the figures are not sufficiently accurate to make distinction possible. Where, however, the figures are good, as in the case of Monro (1755), no doubt can exist, and Monro is most certainly describing Triton and not the Salamander of his title-page. Jacobaeus also calls Triton a Salamander, and here again the Triton determination is beyond question. Indeed nearly all the earlier work labelled Salamander seems to be Triton, in spite of the fact that the name Salamandra was applied to the true Salamander from Gesner onwards, and the differences between *S. terrestris*, or the large earth Salamander, and *S. aquatica*, or the small water Salamander (Triton), were usually recognized.

A statistical survey of the obsolete Salamandra literature shows that most of it is grouped between the years 1815 and 1850. This grouping coincides almost exactly with that of Amphibian literature



generally of the same period, which would indicate that the research of the time was focused on the phylum as a whole and not on any particular member of it.¹

Aristotle, to whom the terrestrial Salamander must have been well known, and who named it *Σαλαμάνδρα*, does not deal with the anatomy of the species. Schneider has suggested that Aristotle's *Κορδύλος* may have been an aquatic or a larval Amphibian, and von Siebold actually refers to the larval Salamander as *Cordylus*, but Leuckart (1823) rightly questions the accuracy of this determination. Albertus Magnus identifies the Salamander with the *Stellio* of ancient authors—the only justification for which seems to be its poisonous nature and the spots on its back.

Belon (1553) appears to have been the first observer to discover the viviparous nature of the Salamander, which, he says, like all vipers, brings forth its young alive. According to Gesner (copied by Aldrovandus and Wurffbain) Belon found that the larvae, to the number of forty to fifty, were born without any foetal membranes, but the latter passage has not been traced in any of Belon's works. Gesner (1554) is the first author to mention *S. atra*. He says that there is a dull black Salamander in the Alps similar in form to the spotted Salamander, and secreting the same white fluid from the skin, but with a short tail. He adds that *Salamandra* is the only one of its kind to exhibit intra-uterine fertilization. Coiter (1575), the first comparative anatomist after Aristotle, describes the skeleton of the Lizard in some detail, and he has also investigated the skeleton of the Salamander, which he says is similar to that of the Lizard. The first confirmation of Belon's discovery comes from Dalecampius (1587). In commenting on Pliny's statement that Salamanders have no sex and are not the result of normal generation, he says that a battered Salamander exuded from all parts of its body a milky venom, and from the ruptured abdomen there emerged over thirty ova, and more than thirty foetuses, which swam actively in water. He also dissected a pregnant female which was full of eggs and foetuses, some of which were incompletely developed, but others were quite advanced and were able to move and swim in water. He therefore concludes that it is false to say, as Pliny does, that Salamanders are generated from nothing. Imperato (1599) carries the same subject farther. He claims that Salamanders pair like Vipers, and at the time of bringing forth they congregate in the neighbourhood of ditches, and await the time of rainfall. They then enter the water, and discharge their foetuses in one day to the number of from

¹ Cf. Cole and Eales, *Science Progress*, xi, Fig. 6, 1917.

twenty to forty. The membranes in which the foetuses are enclosed, after the manner of spiders, are soon thrown off.¹ A figure is given of the larvae, which clearly belong to *S. maculosa*, but no external gills are shown. An early dissection of a female Salamander carried out by Hoffmann *c.* 1642, but not published until 1722, included an examination of the heart, in which only one auricle is mentioned, the abdominal viscera, together with the spleen, gall-bladder, and bile-duct, and certain of the larger blood-vessels. He notes that the uterus is paired, and from it he took thirteen small living foetuses which were black in colour and not yet provided with the yellow markings. Somewhat later, in 1673, Steno describes the two ovaries and fat bodies and also the two oviducts (with contained ova) which he says are not joined at either end.

The first attempt to work out the general anatomy of a 'Salamander' was made by Jacobaeus (1676-86). His little book was severely criticized by Swammerdam, whose own monograph on the Frog was on a much higher plane. A careful examination of Jacobaeus's text, and a comparison of his figures with dissections of Triton, make it quite certain that his subject was Triton and not Salamander. In general his statements are more or less admissible if applied to Triton, but are difficult to understand in relation to Salamandra. He gives for the time a fairly complete account of the abdominal viscera, and makes the interesting observation that the heart beats for many hours after removal from the body, as in Frogs, Toads, and the Torpedo. He figures what might be scattered supra-renal nodules, but from their distribution are perhaps the Malpighian bodies. Almost contemporary with Jacobaeus is the more ambitious and scholarly work of Wurffbain (1677, 1683). He claims to have dissected several terrestrial Salamanders, which hardly accords with the fact that his visceral anatomy is taken almost entirely from Jacobaeus, and his notes on the skeleton from Coiter. He, however, correctly describes the contents of the stomach, which Jacobaeus found to be empty, and mentions for the first time the shedding of the epidermis, but as he says it takes place in water he can hardly have been dealing with Salamandra. He looked for the auditory organ but was unable to find it. Previous statements that the terrestrial Salamander is viviparous are confirmed, and Wurffbain found thirty-four larvae in one specimen. He illustrates the appearance of these larvae, but as no external gills are shown or mentioned, we may suspect that his figures owe more to Imperato than to nature.

¹ Imperato is quite correct in this. The Salamander is normally ovo-viviparous, but the egg membrane may rupture *before* the egg is laid.

A more serious attempt to anatomize the Salamander, this time without any Triton complications, was made by Perrault c. 1680, but not published until 1734. He dissected two specimens—a male and a female. He noted that the black parts of the skin when viewed under the microscope showed a large number of yellow spots which were almost invisible to the unassisted eye. There was no external auditory opening as in Lizards, but the animal could hear nevertheless. The tongue, liver, teeth, gall-bladder, and gut are well described, but the pancreas is assigned a wrong position, and his hepatic duct seems to have been a blood-vessel. Various mistakes and omissions occur in the description of the bladder and urogenital system, and his version of the female genital ducts is simply incomprehensible. It is perhaps remotely possible that his specimen may have been an hermaphrodite. He asserts that, contrary to accepted belief, the Salamander is sexual and has distinct male and female genital organs, however peculiar they may be. He failed to notice that the young larvae had external gills, and he described the heart as having only a single left auricle. Vallisneri (1715) apparently regarded Triton and Salamandra as belonging to the same genus. His remarks on the poisonous white secretion of the skin, its peculiar colour, and the supposed reaction of the animal to fire show that he had the true Salamander in mind, but his anatomical work must have been based on Triton. Thus he describes long lungs which extend the length of the abdomen, he denies that there are four testes, he identifies two penes as in snakes and lizards, and in one specimen he found the stomach to be full of frog's eggs, and in another of fish eggs. Maupertuis (1727) redescribes the 'milk' glands of the skin, and from one female he took forty-two, and from another fifty-four, well-developed active larvae, but he says nothing of the external gills or of the caudal fin. Although the work of Du Fay (1729) relates almost entirely to Triton, he deserves mention as being the first author to describe those very obvious larval structures—the external gills. He found also the 'internal' gills, the gill arches and slits, and made an important contribution to the anatomy of metamorphosis. He was likewise the first to describe the double urogenital papilla of the male Salamander, which he regards as a penis—a structure which, he says, a viviparous animal should possess. He 'presumes' that the terrestrial and aquatic Salamanders are viviparous and oviparous respectively. He traces the passage of the eggs from the ovary through the ostium into the oviduct and so to the exterior. The 'penis' was subsequently described by Latreille in 1800 and by numerous later authors, but others either failed to

observe it or doubted its erectile nature, and Duvernoy even denied its existence.

The celebrated Monro secundus, in his inaugural dissertation (1755), gives us an admirable description of the male genitalia of 'Salamandra'. He mentions a connexion between the genital system and the heart by which the semen is supposed to reach the bloodstream. This may be either Müller's duct, which is always present in the male, or the post-cardinal vein. Monro's paper is the most careful account of the male genitalia and renal organs with their ducts, the cloacal glands (which he notes are not developed in the female), lung and fat body of a Urodele so far published, but the subject was undoubtedly Triton and not Salamander. In the short and little known paper by Zinn published in 1757 there are many brief anatomical notes covering almost all the organs of the body except the nervous system, of which the most important is his discovery of the operculum which fits into the fenestra vestibuli (ovalis) of the ear. He also saw the otolith, and noted the absence of auditory ossicles and an external ear duct. In 1758 Roesel, who died in the following year, was working on an *Historia Naturalis Salamandarum*, which was never completed or published. J. Hermann, in 1789, reported that he had seen the plates, which compared favourably with Roesel's beautiful illustrations of the Anura published in 1758. No descriptions of these plates have been found. Kleeman says that Roesel hoped to publish a work on the Lizards and Salamanders of his native country in the same style as that on the Frogs, but that he died before he was able to complete it.

The genus *Salamandra* was instituted and defined by Laurenti in 1768, and he was the first to name and figure *S. atra* from the Alps—a species first described by Gesner. The name Salamandra occurs in Aristotle, and has been used by many pre-Linnean systematists. It was applied indifferently to any tailed European Amphibian, or even treated as an abstraction without any objective equivalent. Laurenti draws attention to the fact that the Amphibia, being without a diaphragm and ribs, cannot breathe like a mammal, but that by alternate movements of the throat they can empty and fill the lungs with air. He was thus familiar with the idea of the buccal force-pump, but was not aware that this had already been described by Swammerdam in 1667, and also that there was an admirable analysis of buccal respiration in the posthumous works of Malpighi published in 1697. Malpighi indeed was the first to show that when the lower jaw of the frog was severed the lungs could no longer be inflated.

John Hunter's work on the Amphibia, which must have occupied his attention round about the year 1780, but which was not published until modern times, is characteristic of his original and penetrating mind. There are eleven Hunterian preparations of Salamandra still to be seen in the Hunterian museum. They illustrate the abdominal viscera of male and female in some detail, and a *S. atra* is shown with one of the two foetuses to which it is limited, but this last preparation was presented by Buckland and is not Hunterian. Hunter attempts an instructive comparison of Salamandra and Triton in respect of their structure and reproductive habits, with which he exhibits a greater familiarity than his predecessors, and his interpretations are remarkably sound. As usual, however, he did not concern himself with the work of others, and some of his points, though original as far as he was concerned, were not new. In his classification according to the structure of the heart he institutes a group named the Tricoilia (= Reptiles and Amphibians) in which the heart has three chambers—two auricles and one ventricle. This classification was first printed in the posthumous work on the Blood in 1794, but no details are given there, and the complete scheme was only published long after Hunter's death. He included the Salamanders in the group with the two-auricled heart, and was therefore the first to perceive the essential structure of the Amphibian heart.

Blumenbach (1787) is the first author to mention all the points which characterize the larval Salamander, viz. the external gills, the four appendages, and the aquatic, as contrasted with the terrestrial, type of tail. This may appear to be observation of an elementary character, but we have seen that the external gills were completely missed by the earlier naturalists, and even as late as 1800 Latreille was denying their existence, whilst Saint-Julien in 1789 interprets the gills as a pair of long fins, and failed to discover any traces of the limbs. Blumenbach also held that female Salamanders which were for months isolated from males nevertheless gave birth to young, from which he concludes (i) that the eggs are not fertilized after they are laid and that the Salamander is truly viviparous; and (ii) that, as in the case of the fowl, a single act of fertilization is effective for some time. He found that the Salamander was capable of regeneration, and that if a third of the tail was cut off it could be completely, but not quickly, regenerated. The first detailed description of the auditory organ of a Urodele is given by Scarpa (1789), but his observations relate to the aquatic Salamander (Triton). The essential facts are correctly stated, and he realized that Triton

was morphologically not the Reptile it was supposed to be. Townson (1794-5) draws attention to the fact (previously known to Aristotle, Coiter, and Malpighi) that the lungs of Frogs do not collapse when the wall of the cavity in which they lie is opened up. Therefore the mechanism of respiration must be very different from that of the Mammalia. He then proceeds to investigate buccal respiration in Salamandra. He describes and figures a pair of long narrow 'sterno-hyoid' muscles,¹ which arise from the pelvic girdle and are attached to the hyoid. These muscles draw the hyoid downwards and backwards, and thus increase the cavity of the mouth. When they are cut respiration ceases. Other muscles, the constrictors of the pharynx, elevate the hyoid and draw it forwards—thus contracting the cavity of the throat. According to Townson, when the mouth cavity is opened up and the muscles of the hyoid left intact, the hyoid is still drawn backwards and forwards, and the glottis opened and shut, although the lungs remain collapsed; but when the muscles of the hyoid are cut the glottis alone is unaffected, and still continues to open and shut. Townson claimed that the contents of the bladder were as pure as distilled water. It is, therefore, not a urinary bladder, but acts as a reservoir for water which is 'further distributed as their economy may require'.

The first comprehensive treatise to collate previous observations on the Salamander, and combine them with many original observations, is to be found in Cuvier's *Leçons*. In the first edition of this important work the Salamander material relates chiefly to the skeleton and muscles. Between the first and second editions, however, the Salamander must have been further investigated, since the latter edition, which was posthumous and not prepared by Cuvier, includes much additional matter on the species. In the first edition of the *Leçons* (1805) he states that the Batrachian heart has a single auricle and ventricle, and in the second edition (1839) the statement is repeated with the editorial qualification, as regards the auricle, of the word 'apparently'. The editor of the latter edition, G. L. Duvernoy, who had evidently read Davy's paper of 1828, proceeds to add that the auricle is divided into two chambers by a very thin partition, more membranous than muscular, the free border of which penetrates slightly into the cavity of the ventricle. In the tadpole, however, the heart is like that of a fish, and has only one auricle. In the second edition of the *Leçons* Duvernoy (1846) gives a good description of the cloacal glands of Salamandra under the name of 'prostates'. This was presumably based on Rathke. In the *Ossements Fossiles* of 1824,

¹ = rectus abdominis profundus + rectus cervicis profundus of this work.

which appeared between the first and second editions of the *Leçons*, Cuvier adds and codifies the work already published in 1800 in the first and second volumes of the *Leçons*, and he now gives for the first time a very good description with figures of the entire skeleton of Salamandra, which is compared with that of the Frog. His interpretation of the bones of the skull naturally differs from modern usage. For example, he describes the posterior nares as entering the mouth *behind* the vomer, but as Cuvier's vomer is a pre-vomer the position of the internal nares is not as anomalous as he supposed. The Y-shaped or ypsiloid cartilage in front of the pubic symphysis, which he compares with the marsupial bone of Mammals, had been already described, figured, and named by Townson. The Urodele types are somewhat confused in Cuvier's work, and it is not always certain to which of them a particular statement refers.

In Daudin's voluminous treatise on the Reptiles (1803) the Salamanders are correctly located with the Frogs and separated from the Lizards and Reptiles. The idea was not a new one, but hitherto it had not been expressed in any classification. Thus Cuvier compared the Salamanders with the Frogs, but continued to classify them with the Reptiles. That the Amphibia were entitled to independent rank was emphasized in 1806 by Duméril, who instituted the groups Urodela and Anura under the French names of Anoures (Ecaudati) and Urodèles (Caudati) as the two families constituting the Batrachia—the latter term with the spelling Batrachii having been previously introduced by A. Brongniart in 1799. The Latin term Urodela was coined by Latreille in 1825.

Important work on the anatomy and reproductive habits of the Salamander was published by Gravenhorst in 1808 and 1829. The first of these is a short preliminary communication, without illustrations, in which he refers to thirty-one figures of the anatomy of land and water Salamanders which are presumably those published later in the folio work. Gravenhorst's volume includes a useful examination of most of the preceding literature, the mistakes in which he endeavours to correct, and he has very carefully revised the anatomy of the gut and urogenital organs of both sexes. The drawings of the latter organs are particularly good and accurate, and his figures generally are faithfully drawn, and do not include any structure he has not seen and closely examined. He discovered Müller's duct in the male, and shows its forward extension, but did not understand how the seminal fluid reached the vas deferens, since he found no direct connexion between this duct and the testis. Nor does he distinguish between Müller's duct and the vas deferens, but these two

structures are so closely associated in Salamandra that their relations were only understood when the histologist Leydig examined them microscopically in 1853. Judging from appearances in one of his figures Gravenhorst seems to have found the receptaculum seminis—later discovered by Rathke, Leydig, and von Siebold. His figures of the developing larvae are better than those of Funk and Rusconi's earlier drawings. Jacobson (1817) describes the relations of the anterior abdominal and renal portal veins in the Batrachia and Salamander, and concludes, as Townson had done before him, that the bladder in these animals is in no sense a urinary bladder, since its structure is entirely different, and the ureters are not related to it as they should be in a true urinary bladder. A brief but accurate account of the auditory organ of the Salamander was published in 1818 by Pohl. He describes the bony capsule, the external vacuity closed by the 'cartilaginous operculum' discovered by Zinn, and the entry of the auditory nerve. He calls the vacuity the 'fenestra vestibuli' as in modern usage. He describes the three semicircular canals and their ampullae, and gives a figure of the operculum and the fenestra which it closes. C. A. S. Schultze in 1818 was the first to reveal a curious osteological point in the terrestrial Salamander, viz. that the transverse processes of the vertebrae are bifid, and articulate with the bifurcated ends of the ribs. In the same year Meckel published a comparison of the hyobranchial skeleton of Salamandra and Triton, which, however, was based largely on Cuvier. The same author's treatise on comparative anatomy is a useful summary of existing knowledge, but perpetuates many errors. He asserts that there is only one auricle of the heart in the Amphibia, and that it contains mixed blood, but admits that in Salamandra and Triton the auricle is divided by a well-marked constriction into an anterior larger and a posterior smaller section. He mentions that he sought for a carotid gland in Salamandra, but was unable to find it, although he was more successful in other Amphibia.

The third encyclopedic treatise on comparative anatomy to be published in the early years of the nineteenth century was the *Lehrbuch* of C. G. Carus, the first edition of which appeared in 1818 and the second in 1834. Carus had evidently dissected several examples of *S. maculosa* more or less carefully, so that this work is not entirely a compilation. He describes the valve in the nostril¹ which he says is like an eyelid, and noted its relation to buccal respiration. He agrees that the bladder is only a water-holder, and even regards it as a possible respiratory organ, since it is analogous to the allantois of

¹ Not, however, present in the Salamander.

Lizards and Birds. The old mistake that the heart has only one auricle is repeated, but he states correctly, contra Swammerdam, that there are not two carotid glands on each side, but only one. His views on the skeleton are dominated by his adhesion to the vertebral theory, which he accepted in its most extravagant form. The whole work is useful as a restatement and discussion of previous literature. A more important contribution by Carus to Salamandra research is his paper of 1819. In this he describes correctly the parts of the gut, and gives details of the female genitalia. He found the ostium of the oviduct, and wondered how the large eggs could pass through it. Although the eggs develop in the uterus they are entirely free, and there is nothing corresponding to a placenta. Neither is there any connexion between the foetus and the egg membrane. The anterior abdominal vein is interpreted as a persisting foetal structure, and comparable with the umbilical vein of the Mammalian foetus. He gives a good account of the gross anatomy of the larva, including the gut, and believes that the yolk mass is contained within the gut wall, and is thus nothing more than an inflated section of the gut. In fact both the yolk-sac and the urinary bladder or allantois remain within the body wall—unlike the condition found in Mammals. In his last paper dealing with the Salamander (1828) Carus publishes two original figures of the trunk and limb muscles of *S. terrestris*, but the only mention of these figures in the text is to be found in the description of the plates. They illustrate the more superficial muscles of the head, body-wall, limb-girdles, and limbs.

The genius of Rathke was first exercised in an inaugural dissertation on generation in Triton which was published in 1818. Two years later it was expanded and reissued, and now included the Salamander as a closely related form, the two genera being systematically compared. He describes the development of the fat-body and its relation to the general metabolism of the animal. In starved individuals the fat-body dwindles and even disappears, and during the winter it is used up. All the fat in the body of the Salamander is concentrated in its fat-body.¹ The development of the genitalia with their ducts, as far as it can be followed with a lens, is attempted for the first time. The growth of the eggs in the oviduct is given in detail, but he regards them as efflorescences of the ends of the ovarian vessels. His mistake that the eggs escaped through an aperture in the ovary was corrected by Czermak in 1843. A comparison of the finer structure of the ovary and testis led him to believe that from first to last they are identical structures, the adult testis being

¹ In these statements Rathke goes too far.

nothing more than a higher development of the ovary. The spermatozoa are not recognized as such, and therefore a comparison of egg and sperm is not attempted. He is puzzled to discover how the semen passed from the testis to the vas deferens, and had to abandon this question unsolved. He describes and figures a 'gland' associated with the cloaca of the female Salamander which we now know to be the receptaculum seminis. Rathke's paper therefore contains the first undoubted description of this structure. He does not mention that it contains spermatozoa, but neither does he concern himself with the spermatozoa in the testis. The receptaculum seminis of the Salamander, as already stated, was rediscovered by Leydig in 1853, who found (later) that it contained spermatozoa, but it was not adequately investigated until Siebold ascertained its true nature in 1858. Siebold regarded it as a unique structure only occurring in the Salamanders. He overlooked the possibility that the organ might be represented in the male by the pelvic gland, as was suggested later by Blanchard (1881). If the receptaculum seminis is not comparable with the pelvic gland, the cloacal glands of the male have no counterpart in the female. Rathke was the first author to study carefully the male cloacal glands, and he gives good descriptions of both the pelvic gland (*Beckendrüse*) and the anal or cloacal gland (*Afterdrüse*). His views on the nature and functions of these glands have naturally required revision, and the whole situation was reviewed by Blanchard in 1881. Rathke's work is well illustrated, the figures covering the anatomy of the Salamander generally. They are most defective in respect of the urogenital system of the male, the elucidation of which was perhaps beyond the knowledge of his generation. In a later work (1829) Rathke describes for the first time the fragmented adrenal of the Salamander.

In 1819 Schreibers publishes a very good description, as far as external characters are concerned, of the life-cycle of both species of Salamandra. In *atra* he never found more than two foetuses in each female. They possessed very large red gills in the earlier stages, which were almost completely lost before birth. In a later paper (1833) he draws a sharp distinction between the two species in structure, occurrence, and habits. *Maculosa* produces periodically in water batches of forty to sixty young, the average number being forty-six to forty-eight. In captivity they were born within two consecutive days, and all were at the same stage of development and of about the same size, and provided with external gills. On the other hand *atra* never gives birth to more than two at a time. Nevertheless the ovary is relatively as large as in the other species, and as many

eggs reach the oviduct together. Only one, however, in each oviduct develops, the remaining eggs fusing to form a common yolk-mass which serves for the nourishment of the surviving embryo, who is thus the 'assassin of his brothers and sisters' (Duméril). The gills are half the length of the entire body and extend backwards to the hind limb, but they degenerate before birth, and the young are produced in the adult state with scarcely any trace of the gills, and none of the gill openings. This is ascribed to the fact that *atra* lives in situations where water may be scarce or not available, and hence the metamorphosis must be completed within the uterus. Schreibers asserts that he has observed *atra* in captivity coupling in water as in the Frog, and that if the larvae of *maculosa* are forcibly kept under water the metamorphosis may be delayed for many months.

The spermatozoa of the Salamander were first described by Prévost and Dumas in 1821. The work of Dutrochet (1821-2), although it relates to Triton only, may be mentioned as containing the first account of the 'internal' gills of the Amphibian larva. He also makes the suggestion that the regeneration of the limbs and tail is not a case of preformation, but of the epigenetic development of parts much as they were originally produced in the embryo. The ear of *Salamandra* and its semicircular canals were re-described by Blainville in 1822. He says that there is no trace of a tympanic cavity or Eustachian tube, but adds (incorrectly) that these parts are well developed in the larva. He shows for the first time that the operculum which closes the fenestra vestibuli, thereby taking the place of the auditory ossicles, can be moved by a component of a shoulder muscle (*M. opercularis*). Two years later Huschke, also working at the auditory organs of *Salamandra*, confirms the absence of a tympanic cavity and Eustachian tube, and asserts that the operculum is rather a detached portion of the skull (as it is) than a true ear bone. He found that the operculum was elastic, and would spring back into its place after it had been pulled up. He holds that the columella and ear ossicles arise from the anterior gill arches, that the tympanic cavity represents the gill cavity of the fish, and that the Eustachian tube is an inner gill opening.

Dr. J. Davy, the younger brother of Sir Humphry Davy, was the first author after Hunter to throw any light on the structure of the Amphibian heart. He did not examine the Salamander, but his work has general bearings which are too important to be disregarded. In his first communication of 1826 he finds that the heart of toads and frogs consists of two auricles and one ventricle, the auricles being separated by a fibrous septum, and he considers it probable that the

same condition prevails in all other members of the group. In the full paper, published two years later, but dated 2 July, 1825, he states that the auricular septum 'appears' to have muscular fibres, and that there are three semi-lunar valves between the auricles and the ventricle. There is no direct communication between the two auricles. The smaller auricle is associated with the pulmonary veins and the larger one with the venae cavae. The two auricles contract first, then the ventricle, and finally the conical part of the ventricle (= truncus arteriosus), which latter he regards as a second ventricle. It is separated from the rest of the ventricle by three semi-lunar valves, and its cavity contains a fleshy projection or movable septum (= spiral valve). There are further semi-lunar valves between it and the aortic vessels. He asserts definitely that the pulmonary arteries only *accompany* the aortic trunks and are not branches of them. It is not often that observations of such relative accuracy and importance are included in so unpretentious a paper.

The monograph on the Salamander by Funk published in 1827 becomes less impressive the closer it is compared with the work which preceded it. Funk is at his best on the muscles, which had previously not been systematically examined, but the remaining sections of the work, which cover more or less the entire anatomy of the type, are much less satisfactory, even for the time they were written. The historical chapter, however, bears evidence that much labour and knowledge were concentrated on its production—indeed Funk is a better historian than anatomist. He does not touch the cranial nerves, and there are only brief notes on the sense organs, nor did he succeed in finding the sympathetic. The otolith is identified as a rudimentary auditory ossicle, and he has no observations to offer on the lymphatic system, the investigation of which he admits is beyond him. There is a physiological section dealing with the effects of various gases and vapours on respiration. The most inaccurate parts of Funk's monograph are those which deal with the vascular system and the brain. He only distinguishes two chambers in the heart—an atrium and a ventricle—an error which induced him to make the pulmonary veins discharge into the vena cava. He found no valves in the heart, and his account of the distribution of the vessels is defective both as regards observation and interpretation. He appears to have missed completely the carotid arch—his *first* pair uniting to constitute the dorsal aorta, and the veins are only partly, and not accurately, figured. He even seems to have confused arteries and veins. Rusconi later revised this part of Funk's work, and corrected his mistakes. As regards the brain, the figures are imaginative and

have little relation to the objects they represent, and his description is too meagre to throw any light on his methods, or to suggest an explanation of his errors. Funk's account of the gut and male and female genitalia is much better. He describes a three-lobed testis (it is usually two-lobed), and he made a serious attempt to unravel the relations of the genital glands and ducts—a full understanding of which, however, was beyond the technique of his time. Two years later Gravenhorst materially improved on Funk's descriptions of the genitalia.

Gachet's paper of 1827¹ is an interesting first-hand account of the feeding and reproductive habits, metamorphosis, and regeneration in the Salamander, but it contains little that is new. A year later Siebold published his inaugural dissertation on the Salamander and Triton. It is a remarkable and important maiden effort. He is the first to trace accurately and in detail the *metamorphosis* of the larval hyobranchial skeleton and musculature into that of the adult. He gives a very good description with figures of the larval and adult states, and also an excellent illustrated account of the anatomy of metamorphosis, especially as regards colour, gills, operculum, and tail. It is a very instructive study in the physiology of adaptation, and of the phenomena which accompany the change over from aquatic to terrestrial life. He shows further how metamorphosis may be controlled or modified by varying the conditions. A sketch of the development of the internal organs is included, and there is a section on the myology of the tongue and hyoid, in which the movements of the tongue are explained.

The first statement of the discovery of the posterior lymph hearts of the Frog was made by J. Müller in September 1832. A year later the anterior lymph hearts were found, not only in the Frog and Toad but also in the Salamander and Lizard. Müller observed the contraction of the hearts, and noted that the rate was peculiar to the organ, and different from that of the heart and lungs, nor were the pulsations of the two sides synchronous. The hearts contained a clear lymph and not blood. The methods employed by Müller in the investigation were mercury injections and inflations, and he claims that a pulsating *lymphatic* organ had not previously been seen. He states that the posterior lymph hearts are difficult to find in the Salamander, but that they are in the same position as in the Frog. Panizza had already seen the lymph hearts of the Frog in 1830, but had not

¹ The volume is dated 1827, but the author refers to an incident which happened in April 1828. He states that his plates were being published elsewhere, but so far no such publication has been traced.

observed them in the living animal, and hence was unaware that they pulsated and were therefore hearts.

Windischmann (1831) dissected five Salamanders, and describes the 'finer' structure of the auditory organ. He was the first to observe that the fenestra vestibuli (ovalis) is closed by a membrane to which the operculum is related, the operculum itself not occurring in the larval Salamander. His figure of the labyrinth is crude and distorted, but he noted the absence of a cochlea and of the fenestra rotunda. Bischoff (1832) gives a small and poor figure, but hardly any description, of the dorsal surface of the brain of *Salamandra*—a part of the animal which had so far been almost entirely neglected. In 1832 Martin Saint-Ange confirms the existence of two auricles in the heart of the *Anura*, and adds that in the Salamanders also there is a small but distinct left auricle.

The monograph by Panizza on the lymphatic system of Reptiles published in December 1833 is one of the most important of the earlier works dealing with the comparative anatomy of this system. He used injections of mercury, and coloured masses such as size, and his material included representatives of most orders of Reptiles and Amphibia. He discovered the anterior and posterior lymph hearts independently of Müller, and proved by repeated experiments that, as the lymphatics did not open into the gut and were peripherally distinct from the true blood-vessels, they must therefore be regarded as an independent system. He found that in *Salamandra* the lymphatics were developed to a prodigious extent, and that the networks were of astonishing minuteness. On the other hand the main trunks were unusually capacious, and communicated on each side with the anterior vena cava by valved apertures. There were further openings posteriorly into the pelvic veins, and at this point a contractile posterior lymph heart driving the lymph into the veins might be present. He did not, however, find the latter heart in *Salamandra*. The main lymphatic cistern in *Salamandra* extended from the anus to the pylorus, expanding as it passed forwards. In the abdomen it divided into two sinuses associated with the genitalia, which united again anteriorly to form the thoracic duct. The latter bifurcated in the neighbourhood of the heart, each division receiving the lymphatics from the region of the fore-limbs and head of its side, and opening finally into the subclavian of the same side by two or three small apertures. In a later paper published in 1845 Panizza regards the respiratory process in *Salamandra* as one of deglutition of air, and he develops in detail the theory of the buccal force-pump and explains the physiology of the muscles and skeleton concerned.

The backward extension of the sternohyoid muscle to the pubis is not associated with the extra length of the lungs, as suggested by Haro (1840), but is due to the fact that there is no fixed sternum as in the Frogs. The sternal region of the pectoral girdle in Salamandra moves with the limbs, and therefore offers no *point d'appui* which could serve for muscular attachment. In the following year Panizza is engaged on an experimental investigation into the flow and velocity of the respiratory current in the larva of the Salamander. He describes the action of the cilia in directing and maintaining the current, and examines the conditions which affect the vitality and irritability of the ciliary mechanism.

Dugès's work on the osteology and myology of the Batrachia (1834) includes some observations on the terrestrial Salamander. The figures are good and accurate, but not accompanied by adequate descriptions. The object of the paper is to compare the condition of the skeleton and muscles of larva and adult. Some structures are peculiar to the larva and others to the adult, but those which occur in both undergo modification during metamorphosis. The figures are the most detailed and accurate of these two systems so far published, but the Urodeles have not been so carefully studied as the Anura, and Triton figures much more largely in the paper than Salamandra. Reichert's work of 1838 also relates to Triton, but it is very important from the point of view of the development and morphology of the skull and visceral arches in the Urodela. Henle is the first author to investigate the anatomy of the larynx of Salamandra, which he describes in a noteworthy and accurate work published in 1839.

We now reach the numerous and striking contributions to Salamandra literature for which Rusconi is responsible. The first was published in 1839, and the last, which was posthumous, in 1854. Owing to the fact that Rusconi coloured the plates of his papers with his own hands, and was unable or unwilling to devote the necessary time to this task, several of his most important writings are very rare, having been limited to editions of 100 copies, and in one case of only 24. In his first paper Rusconi states correctly that in *S. maculosa* the sexes couple on *land* and not in water, and therefore the sperm cannot reach the oviducts mingled with water as had hitherto been accepted. He further denies (this time wrongly) that only two larvae may be produced at a time in a Salamander, thus showing that he was not aware of the difference in this respect between *maculosa* and *atra*. In fact he declines to believe that there can be such a considerable distinction between the species. He was greatly puzzled when he

discovered that segmenting eggs occurred in the oviducts *before* pairing had taken place, nor did he succeed in throwing any light on the problem of fertilization in the Salamander. In his posthumous treatise on the terrestrial Salamander, which may be considered next since the work was done before 1839,¹ he does not seem to have been aware that the Amphibian heart has two auricles. He definitely says it has not in Spelerpes, and as regards Salamandra he always uses the term atrium in the singular. He gives a very full account, accompanied by excellent figures, of the development of the external characters, from the segmentation of the egg up to the adult stage. His outline of the development of the internal organs, such as the gut, nervous system, and skeleton, is a very definite advance on the standard of such work at his time. The anatomy of metamorphosis is accurate and more detailed than any previous description, and he is especially admirable on the metamorphosing skull, and on the changes undergone by the muscular and vascular systems. He describes and figures the carotid gland,² which he says 'is actually a consequence of the shortening of the artery at the moment of metamorphosis'. He did not succeed in finding the lymph hearts, but describes, and beautifully illustrates, the lymphatics of the gut and bladder. Perhaps, however, his most interesting discovery is that of the pronephros and segmental duct, which he describes and figures under the name of 'Wolffian body'. Leydig also figures these structures in the Salamander larva in 1857. In 1841 Rusconi becomes involved in a controversy as to whether the blood-vessels of the Salamander are morphologically inside or outside the lymphatics. For some years he adhered to the former view, and insisted that the blood-vessels were in direct contact with the lymph right up to their smallest branches in the skin. Panizza, on the other hand, maintained that the arteries were only invaginated into the lymphatics, and were related to them as the heart was to the pericardium. The controversy was prolonged for some years, Rusconi repeatedly claiming that his double and triple injection methods were superior to the mercury injections of Panizza. In fact he was so convinced of the soundness of his attitude that he began to get interested in questions of priority, and to argue who was the first to discover this mare's nest.

¹ This monograph was actually completed in 1839, when it was partly set up in type. Rusconi, however, postponed publication in order to revise it, but he did not live to complete this task.

² The carotid gland of Amphibia was discovered in the Frog by Swammerdam in the seventeenth century (published 1738). He, however, describes and figures *two* on each side, the second apparently being the thyroid gland.

In the end, however, he had to admit that he was wrong. First of all he found that a vein might be accompanied by a *pair* of lymphatics, and this raised doubts whether he might not be mistaken *in some cases*. Finally he acknowledges that in the Salamander the blood-vessels are enclosed by a *double* wall, and are hence morphologically external to the lymph cavities, being related to them as the gut is to the abdominal cavity. One valuable result of this otherwise futile controversy was that it induced Rusconi to look closely at the lymphatic system of Salamandra, which resulted in many valuable facts being added to our knowledge of the system.

It is surprising that up to this time no serious attempt had been made to investigate the nervous system of the Salamander. The first to do so was Fischer (1843), who describes the cranial nerves in a work which is remarkably accurate for the time it was written. He did not find the fourth pair of nerves, and believed that its eye-muscle was supplied by a branch from the trigeminus, but he was more successful with the sixth nerve in spite of its small size. He was unable to discover more than the slightest traces of the sympathetic in the Salamanders, and believed that it was of much less importance in them than in the Anura. This conclusion is not surprising in view of the considerable difficulties which confront the investigator of the sympathetic of Salamandra. Fischer's description and figure of the fifth, seventh, and tenth cranial nerves are detailed and accurate. He points out that the fifth and seventh nerves are separate in the Salamander but fused in the Anura, and he correctly describes the association of the glossopharyngeal with the vagus and its anastomosis with the facial. He also understood the mutual relations of the auditory and facial nerves. Meyer's work on the lymphatic system of Amphibia (1845) is largely a compilation from Panizza and Rusconi, but he found two pairs of anterior lymph hearts in the Salamander which had not previously been seen. The longitudinal duct coursing parallel with the inner margin of the kidney into which the vasa efferentia open was first described by Bidder in 1846, and is often referred to as Bidder's duct. The discovery of this duct made it possible to solve the old riddle as to how the male sperm escaped from the body, which had puzzled so many previous workers. The spermatozoa themselves were re-described by Czermak in 1848. This author, who had previously (1843) explored the differences between *S. maculosa* and *S. atra*, gives a remarkably accurate description, with figures, of the complex spermatozoon of the Salamander, and he even attempts to work out the details of spermatogenesis, as well as the mechanics of the tail and its undulating membrane. Many

subsequent accounts are in fact less reliable than Czermak's. The undulating membrane of the Salamander sperm had previously been imperfectly observed by Wagner, Siebold, and Dujardin in 1837-8. Dujardin interpreted it as a very tenuous free spiral thread wound round the axis of the tail. This was corrected by Pouchet in 1845, but Czermak was the first to give a classic description of the curious spermatozoon of the Salamander. In 1853 Leydig described and figured the pineal body and sympathetic ganglia of *Salamandra*, and was the first to note that the Müllerian duct of the male was not a branch of the Wolffian duct, but ran alongside it, the two being enclosed in a common membrane. He was, however, wrong in stating that the Müllerian duct opened posteriorly into the Wolffian duct. The sense organs of the lateral line were first described in aquatic Amphibia by F. E. Schulze in 1861, and again in 1870. Leydig (1868) discovered these organs in the larval Salamander, and they were re-described by Malbranc in 1875. Leydig gives a good figure of the larval *S. maculosa* showing the number and distribution of the neuromasts on the head, body, and tail. The histology of the organs is also illustrated, but the methods available at the time were inadequate for this purpose. It was only thirty years later that Maurer successfully analysed the structure of the amphibian neuromast, and suspected that on metamorphosis the lateral line organs were eliminated from the make-up of the species.

F. J. COLE.

BIBLIOGRAPHY OF THE HISTORICAL INTRODUCTION

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I

TAXONOMY, LIFE-HISTORY, AND GENERAL

TAXONOMY

1. Characteristics of Class, Order and Sub-Order.

THE Salamander, by virtue of its naked glandular skin devoid of scales, its aquatic larva, its three-chambered heart (two auricles and one ventricle), two occipital condyles and the absence of any amnion or allantois around the developing embryo, is placed in the *Class Amphibia* among the vertebrates.

The retention of the tail by the adult and the possession of limbs of approximately equal size confine it to the *Order Urodela* or *Caudata*, while the complete metamorphosis, and the backward extension of the pre-vomerine teeth to well behind the internal nares, limit it to the *Sub-order Salamandroidea*.¹

2. The Family Salamandridae.

This Sub-order comprises three *Families*, the *Salamandridae*, the *Amphiumidae*, and the *Plethodontidae* (mostly American Urodeles). The Salamander belongs to the first of these families, which is characterized mainly by the shape of the pre-vomerine teeth, by the opisthocelous vertebrae, and by one or two other skeletal features of minor importance. The *Family Salamandridae* is again roughly divided into 'Salamanders' and 'Newts', the former being completely terrestrial in the adult stage while the latter show strongly marked aquatic tendencies throughout life. All are completely caducibranchiate in the adult phase. The family comprises some eight genera, namely, *Salamandra*, *Chioglossa*, *Triturus* (Triton), *Tylotriton*, *Pachytriton*, *Pleurodeles*, *Euproctus*, and *Salamandrina*.

3. The Genus *Salamandra*.

The *Genus Salamandra* is distinguished by the 'S' shape of the backward prolongations of the pre-vomerine teeth, together with the subcircular tongue free at the edges, and the prominent 'paratoid' cutaneous glands behind the eyes. The hands are four-fingered and the feet are five-toed, while the tail is rounded in section, and there is no fronto-squamosal arch. The genus contains four species

¹ The classification of Noble (1931) is followed here.

of which two are European and two Asiatic. The two former are well known and are *Salamandra salamandra* (better known as *S. maculosa*), the Spotted Salamander, and *S. atra*, the Black or Alpine Salamander. The Asiatic species are *S. caucasica* and *S. semenovi*, both of which inhabit mountainous districts and are known from a few specimens only—particularly the last named. It is to the first named of these four species that the present work is confined, but a brief account of the general characteristics of the other three may not be out of place, and they will accordingly be discussed in the reverse order to that given above.

4. *Salamandra semenovi*.

Salamandra semenovi was first described by Nesterov in 1916. It is of approximately the same size, or perhaps slightly smaller than the Spotted Salamander, and inhabits the mountains of Kurdistan and Perso-Turkey at an altitude of about 5,000 ft. (Pl. XXV, fig. 83). Nothing appears to be known of its anatomy. It is characterized by the markings which are small and greenish-yellow.

5. *Salamandra caucasica*.

Salamandra caucasica was first described by Waga (1876) under the name *Exaeretus causicus* and its inclusion in the genus *Salamandra* is due to Boulenger (1882). It is rather more slender than the Spotted Salamander, while its tail has a very much greater relative length and contains some fifty-three vertebrae against twenty-two to twenty-five for *salamandra*. The markings are deep orange in colour on a pure black ground and show a strong resemblance to those of *S. salamandra*, *forma typica* (see p. 13). The male is characterized by the possession of a prominent dorsal hook at the base of the tail. As its name implies this species inhabits the Caucasian mountains, to which it appears to be confined (Pl. XXV, fig. 83).

6. *Salamandra atra*.

Salamandra atra has been known from early times. It is restricted to the European Alps over a vertical range extending from about 2,500 to 9,000 ft. (Pl. XXV, fig. 83). It is rather smaller than *S. salamandra* and is distinguished from it by the absence of any yellow or orange markings to interrupt its uniform black colour, and by the relatively shorter tail. Normally this species bears only two young at a time, and these are devoid of gills and are not deposited in water as in the case of the other species, but are fitted from the first for a terrestrial existence. Schwalbe (1896) gives an excellent

account of the 'intra-uterine' development of this species, and shows how the gills have become adapted to effect a gaseous exchange with the maternal capillaries in the 'uterine' wall and to absorb nourishment from the surrounding yolk mass formed by the degenerating eggs which fail to develop.

7. *Salamandra salamandra*.

The name *Salamandra* is of ancient origin and is probably derived from the Arabic *samandar*, by which term the animal is still popularly known in Arabia and Persia. It was applied to this species as a generic term in quite early times (see Historical Introduction). Nevertheless the tenth edition of the Linnaean *Systema Naturae* (1754) from which all modern nomenclature starts—or is supposed to start—describes the animal under the name *Lacerta salamandra*. In 1768 Laurenti quite rightly removed it from the genus *Lacerta* and re-established the older *Salamandra*, but unfortunately the same author also at the same time, and without any justification, changed the specific name to *maculosa*, and this name seems to have become inseparably associated with the animal, since it still persists, although by the rules of priority the Linnaean species should stand. A number of authors have pointed out this discrepancy. One of the earliest of these is Lönnberg (1896), and one may well echo his lament when, in describing the Linnaean type-specimens of Birds, Batrachians, and Fishes in the Zoological Museum of the Royal University in Upsala, he says under the heading *Salamandra maculosa*, Laurenti, 'It would seem provoking to change such an old name, but according to the rules the name ought to be *Salamandra salamandra* (Linnaeus)'. The species is characterized by the shape of the pre-vomerine teeth coupled with the yellow markings on the body. A detailed consideration of the external characters and chief varieties of the species is given in the next section (p. 13).

LIFE-HISTORY

The general features of the life-history and development of the Salamander, such as its habit of bringing forth fully developed larvae (instead of eggs), which subsequently pass through an aquatic phase before metamorphosing into the terrestrial phase characteristic of the adult, have been fairly well known since early times. Nevertheless some puzzling details remained unexplained for a long time, and, even now, further observations concerning fecundation would not be superfluous.

1. Fecundation and Fertilization.

One of the earliest writers to make observations on the development of the Salamander was von Schreibers (1819 and 1833), who correctly observed the method of deposition of the young, but was mistaken as to the mode of impregnation of the female by the male which he thought took place in water. Rusconi (1839) was the first to observe the correct method of copulation, which normally takes place on land, although he was quite at a loss to explain how segmenting eggs came to be present in the oviducts *before* copulation had taken place—a paradox which took many years to solve. Rusconi's paper seems to have been overlooked by most subsequent observers. The discovery of the receptaculum seminis in the female by von Siebold (1858), although only indirectly concerned with fecundation, nevertheless proved to be of great importance in furnishing the ultimate explanation of the mystery which baffled Rusconi. The next observer to discuss the mating of Salamanders was Zeller (1890-1), who confirmed the observations of von Siebold that one act of coition apparently sufficed to fertilize more than one batch of eggs. It was thought that the function of the receptaculum seminis was to hold a reserve of sperms for future use, i.e. that it was analogous to the receptaculum seminis of an insect. This view was also supported by Paratre (1894). Zeller believed that copulation took place at the time of deposition of the young because he found that the receptacula of the females were then full, and he also found spermatophores in the water with the larvae. Five years later Schwalbe (1896) published a very careful and detailed account of the life-history and development of the two European Salamanders, prefaced by an equally clear and lucid review of the previous observers. Schwalbe's account is the first really adequate statement of the facts, which subsequent observers have confirmed, but to which they have added only minor details. Schwalbe finds that locality and external conditions have some influence on the actual times of deposition, copulation, &c., but that on the average fully developed embryos are found in the oviducts of the females from May until June, and then again in October and December. He also showed that sperms may be found in the receptacula in May but *not in June*, and then again from July to November, copulation having taken place during July. Thus he established the important fact that the *sperms must winter in the receptaculum seminis of the female*. He also showed that fertilization occurs high up in the oviducts. The key to the mystery which Schwalbe has thus provided is that the sperms received

by any female in a given season do not *immediately* pass into the oviducts to fertilize the eggs, but pass into the receptaculum seminis and remain there through the winter to fulfil their ultimate purpose in the following May or June. Thus the segmenting eggs which Rusconi found to be present in the oviducts at the time the sexes were pairing were those fertilized by the sperms received during the amplexus of the previous year.

An excellent account of the pairing is given by van Leeuwen (1907), who observed the act in his vivarium. He states that it may occur at any time from June to September (or even in October if the weather is warm) and he only saw it occurring in the evening, and on land. Van Leeuwen describes the male pushing his nose under the hind-legs of the female and working his body forwards until his head is directly under hers. He then embraces the fore-limbs of the female with his own fore-limbs and, with a quiver of the body, deposits a spermatophore on the moss. The male then rotates the posterior part of his body through 90° but still retains his hold of the female, who then lowers her cloaca on to the spermatophore and receives it therein. The spermatophores are described by the same author as transparent yellowish pyramids of gelatinous consistency, about 8–10 mm. high by 4–6 mm. broad, and are deposited with the sharply pointed apex directed vertically upwards.

Kammerer (1907) agrees with van Leeuwen, but has also seen the male approximate his cloaca to that of the female and pass the spermatophore directly into it. He also claims to have seen copulation occur in water as well as on land, and says that then no such approximation of the cloacae occurs. His observation remains unsupported by any other observer.

The segmentation of the egg and the early development were first studied by Kupffer (1879), Benecke (1880), and Grönroos (1895 and 1898), the work of the last-named being the most detailed. In spite of the large amount of yolk present, segmentation is holoblastic but is unequal.

To summarize the essential facts that have been thus laboriously unravelled we may say that the larvae are born in early spring from April to May or June, while they have been observed as early as the 16th of January (Paratre, 1894), the exact period depending on local conditions. Ovulation then occurs, and the eggs thus released are fertilized high up in the oviduct by sperms which have wintered in the receptaculum seminis of the female. Shortly afterwards, during July to September, pairing takes place, and the sperms then received enter the receptaculum seminis and are stored for use in the following

year. The amplexus thus normally occurs while there are segmenting eggs in the oviduct, but whether this is *always* the case is uncertain, neither is there any evidence as to whether the sperms are *able* to fertilize the eggs immediately they leave the male, or whether the period of rest in the receptaculum seminis is essential, and if so what changes, if any, they then undergo. The embryos developing from the eggs fertilized in June have attained full maturity by the autumn, but they are normally carried over in the 'uterus' until the following spring, i.e. for a total period of ten to twelve months. Under favourable circumstances, however, two batches of larvae may be deposited in the same year, and both copulation and deposition of larvae *may* occur at almost any period of the year except during the winter.

2. Deposition of Larvae.

The female deposits the larvae in water, usually in the springs and small streams which abound on the lower slopes of the mountains of central Europe. She does not enter the water bodily, since the adult Salamander is unable to swim and would speedily drown if totally immersed in water beyond its depth, but merely remains at the water's edge with her cloaca and tail submerged. Deposition may occur at intervals over a period as long as two days. The total number of larvae deposited by any female during this period varies from twelve up to as many as seventy-two (Fatio, 1872). Such high numbers are, however, rare and the average may be taken in the region of thirty, and they occur in approximately equal numbers in each oviduct. Dead larvae in various stages of development, and of degeneration, are by no means uncommon and are deposited together with the living ones. The embryos remain within the vitelline membrane until the very moment of deposition, and may in fact actually be 'laid' within it, but normally the act of extrusion ruptures the membrane and allows the larva to swim free. The empty membrane is then pushed out from the cloaca by the succeeding larva. The Salamander is thus ovoviviparous rather than strictly viviparous, that is to say, it lays eggs but the eggs have previously developed within its body to hatching-point before their deposition. The embryo feeds exclusively on egg yolk. Kaufman (1913) finds that the number of degenerating larvae is proportional to the length of the 'uterus' and the number of embryos, and she therefore concludes that the death of these larvae is due to pressure. She also finds that the weight of a full-grown embryo is 1.6 times the weight of the egg from which it developed, and since it is independent

of the mother and does not leave the vitelline membrane, she concludes that the increase in weight is due to the absorption of water. Monsters are not uncommon (cf. Kaufman, 1913; Stadtmüller, 1930, and others). Deposition often occurs at night, and Schreiber (1912) supposes that the act must often be fatal to the females, since he frequently finds dead adults near the water containing young.

3. The Larvae.

The larvae are about 25–30 mm. long at birth, of greyish-brown colour dorsally and greyish white ventrally, flecked with arachnoid patches of black pigment. They possess four fully developed limbs, and external gills, and are adequately fitted for an independent free existence. They are very active and commence to feed at once. Their normal diet consists of small Crustaceans, e.g. *Daphnia*, Cyclops, and aquatic insect larvae, worms, &c. In captivity they flourish well on the Enchytraeid worms sold by aquarist dealers if their natural food is not available. They take these from forceps with great avidity, and will also take small earthworms cut up, or small shreds of meat, provided that the food offered is made to *move*. The hyoid and four branchial arches are represented in the visceral skeleton, and they possess four gill-slits in addition to the external gills.

4. Metamorphosis.

They grow slowly and attain a length of 55–65 mm. in about 3–5 months, when they metamorphose and leave the water. The chief external changes noticeable just prior to metamorphosis are the appearance of yellow pigment, the approach to adult coloration, and the dwindling of the external gills. The loss of the swimming membrane on the tail follows immediately, and the head assumes the adult shape through the advent of the paratoid glands. At the same time profound internal changes have been going on. The cartilages and muscles of the two most posterior branchial arches are normally lost entirely, but the arteries and nerves remain. The tongue also changes completely, the primary larval tongue being replaced by the secondary adult structure (cf. p. 263), while the eye has had to become adapted to see in air instead of in water. It is probably on account of these considerable changes in the organs associated with gustation and deglutition that the larvae show great reluctance to eat for a short time just preceding and immediately following metamorphosis. Of the internal factors which affect the inception and rate of metamorphosis the secretion of the thyroid glands takes the first place, while

the principal external factor is temperature, which has a marked positive influence. Larvae born in the autumn may remain unchanged right through the winter.

The Salamander does not reach sexual maturity until 4–5 years after metamorphosis, by which time it will have attained a length of rather less than 200 mm. Ahl (1930) gives 285 mm. as the maximum length, but this must be regarded as exceptional, 150–200 mm. being much more common.

5. Habits of the Adult.

The adults are rarely seen during the day-time except after a warm thunder shower, when they may suddenly appear in vast numbers. Otherwise they spend the day under stones, in holes, or under moss or fallen tree-trunks, and come out at dusk to feed. Their normal diet consists largely of insects, e.g. beetles and beetle larvae, and also slugs and worms, but Jacobshagen (1914) reports finding considerable quantities of moss and other plants in the stomachs of some individuals. Schreiber (1912) says that *Salamandra salamandra* usually occurs on sandstone and marl, and is rarely found on sandy or chalky bases. They frequently occur in pine forests on the lower slopes of the mountains below 3,000 ft., and rarely up to 4,000 ft. During the winter they congregate in large numbers, often several hundreds together, under an overhanging rock, or in a hollow tree-trunk or some similar place. They get sluggish in cold weather, but their hibernation is only slight, and they not infrequently come out during a warm spell. In general they favour moist places and a humid atmosphere with moderate temperature, and shun the sunlight. No data are available concerning the length of life in nature, but records have been made which show that individuals have lived in captivity for as long as 18 and 20 years (Ahl, 1930; Mehlsheimer, 1911).

6. Geographical Distribution.

The geographical distribution of the species is fairly well indicated in the next section which deals with the several varieties. Schreiber (1912) gives $53\frac{1}{2}^{\circ}$ N. as the northern limit, i.e. a line drawn from Lauenburg through Lüneburg and Bremen to Oldenburg. From here it spreads south-westwards through Holland and Belgium, over France, Spain, and Portugal. Southwards it is found all over Germany and Austria, in Italy and on the Balkan peninsula, in Greece and Turkey. It does not extend eastwards of the Carpathians. Isolated instances of its occurrence have been reported from

as far south as Palestine, Algeria, and Tunis. Very favourite localities are the Hartz mountains and the Heidelberg district of Germany, as well as many parts of the Black Forest, where it is very common (Pl. XXV, fig. 83).

Good accounts of the life-history and habits of the species have been given by Gadow (1901), Werner (1912), and Schreiber (1912), the last named being particularly detailed.

7. Parasites and Diseases.

The most troublesome disease to which Salamanders are subject in captivity is that caused by a fungus, *Monilia batrachea*, Scott, which first attacks the lips (the hands and feet are first attacked in Frogs and Toads), causing open sores to appear. If unchecked the fungus finally ramifies throughout the body, even to the internal organs, e.g. liver, kidneys, &c., and is fatal. It is very contagious and the only effective method of sterilization of vivaria, apparatus, &c., is the painter's blow-lamp, or if accumulator jars are used (and these make by far the best vivaria and are least likely to become infected) *repeated* scrubbing with absolute alcohol has proved effective. The disease *is* curable, if taken in time, by painting the parts affected with 'Mercurochrome' applied with a camel-hair brush about three times a week. Cases must of course be isolated immediately.¹ The aetiology of the disease has been worked out by Scott (1926).

Of the animal parasites of the Salamander the *Protozoa* are represented by a coccidian, *Eimeria salamandrae*, Steinhaus, which infests the epithelial cells of the gut. Among the Helminths representatives of the Trematodes, Cestodes, and Nematodes all occur. Von Linstow (1878-89) gives the following:

TREMATODES.

- Distomum cygnoides*, Zed. in the urinary bladder
- Distomum crassicolle*, Rud. in the intestine and rectum
- Distomum endolobum*, Duj. in the intestine
- Distomum glabrum*, Creplin. in the intestine

NEMATODES:

- Oxysoma brevicaudatum*, Zed. in the intestine
- Strongylus auricularis*, Zed. in the intestine
- Nematoxys commutatus*, Rud. in the intestine

¹ The author is indebted to the late Dr. Joan Procter, formerly Curator of Reptiles at the Zoological Society's Gardens, Regent's Park, London, for the practical notes on this fungoid disease, which are the outcome of experiments carried out in her laboratory.

Among the Cestodes *Taenia dispar* has been reported by Fuhrmann (1896). Von Linstow's nomenclature is of course obsolete. For example his *Oxysoma brevicaudatum* is almost certainly the worm now known as *Aplectana brevicaudata*, and *Nematoxys commutatus* is probably *Cosmocerca commutata* (Dies.), since specimens referable to these genera have been found during the present investigation, together with the trematode *Brachycoelium salamandrae* Frölich, which certainly represents v. Linstow's *Distomum crassicolle*. Ecto-parasites seem to be entirely absent.

GENERAL LITERATURE.

So far there have been two monographs devoted to the anatomy of the Salamander—the first by Funk (1827) which has been dealt with in the Introduction, and the second by Rusconi, commenced in 1839 but not published until 1854, after the death of the author. These two works must be considered as to a large extent complementary. Rusconi corrects some of Funk's mistakes—notably with regard to the vascular system—and fills in some of his omissions. Of these latter the most noteworthy is the account of the anatomy of the larva and of the changes which take place during metamorphosis. He also deals at some length with the lymphatic system, with the life-history, and with the habits of both larva and adult—topics scarcely touched upon in Funk's account.

Of the other literature of a general nature must be mentioned the 'Amphibia' in Bronn's *Klassen und Ordnungen des Thierreichs*, written by C. K. Hoffmann (1873–8), in which frequent references are made to *Salamandra*, but which is rather a compilation of existing knowledge than an original contribution. Most of the original material it does contain had been published previously elsewhere. Of a similar nature is Noble's recent work on the *Biology of the Amphibia* (1931). Osawa's account of the anatomy of *Cryptobranchus* (1902) and Gaupp's *Anatomie des Frosches* (1896) have been found to be of considerable use for comparative purposes.

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II

EXTERNAL FEATURES AND VARIETIES

EXTERNAL FEATURES

THE external form of the Salamander is one of the simplest which it is possible for a terrestrial, tetrapodous vertebrate to have. The *head* is broad and flattened like that of the Frog, but the snout is rather more rounded. The eyes stand up prominently from the surface of the head, while the small *external nares* may be seen in front of them on either side of the snout. The *naso-lacrymal duct* opens to the exterior at the anterior corner of the eye by means of a fine pore which is visible only by the aid of a lens. The apparent gape (see also p. 262) extends to a little behind the posterior corner of the eye, and the upper jaw slightly overhangs the lower. On the dorsal surface of the head, just behind the eyes, is a pair of large reniform protuberances, the *paratoid glands* (see also p. 292). They are very characteristic of the animal. There is no true *neck* but there is a slight narrowing of the contour behind the head, due largely to these paratoid glands, while ventrally there is a distinct fold in the skin marking off the head from the pectoral region. This is the *gular fold*, and represents the line of fusion between the larval gill cover, or operculum, and the skin.

The *trunk* is roughly cylindrical, while the sides of the body present a wrinkled appearance due to the fact that the skin is closely adherent to the myosepta but free in between.

The *tail* tapers, at first rapidly, and then more gradually, and finally terminates in a blunt point. It is very slightly flattened laterally.

Extending from behind the head to the tip of the tail, in the mid-dorsal line, is a double row of cutaneous poison glands of a similar nature to those forming the paratoids. These series of venom-secreting glands are dealt with in more detail on p. 292.

The *limbs* are relatively small, particularly the fore-limbs. Thus mechanically, as well as in many other ways, the Salamander is truly intermediate between the piscine structure, where practically the whole of the animal—apart from the skeleton—is composed of segmental body muscles and viscera, and that of the typical land vertebrate, in which the muscles associated with the limbs tend to predominate over those of the trunk and tail.

The total body length of adult specimens, including the tail,

varies from about 120 mm. to 170 mm., according to age. Of this the tail, or post-sacral region, accounts for rather less than one-half, the proportion being something like 75 : 80. The males tend to be rather smaller than the females, but the sexes are more easily distinguishable externally by the appearance of the cloaca, which is quite flat in the female, but swollen and tumid in the male. This difference is more marked in the breeding season, but a little practice makes it readily distinguishable at any period.

The *gait* of the Salamander is very blundering and clumsy, and when the fore-foot is lifted from the ground the whole body is tilted so as to assist the movement. Then the limb having been moved forwards, the animal 'flops' over on to that side and repeats the process on the other. In this way the movement at the shoulder-joint, in a vertical plane, is very slight. The pelvic limb shows rather more movement in this direction—nevertheless there is a strong tendency for the back of the foot to be dragged along the ground as it moves forward. The sector described by the femur in a horizontal plane lies almost entirely anterior to the transverse plane across the acetabula; in other words, when the femora are fully retracted they are approximately at right angles to the trunk—while when they are drawn forwards to their fullest extent the limb lies close alongside the body. In spite of its apparent clumsiness when seen under ordinary conditions stalking around a vivarium, the Salamander can at times move with astonishing rapidity, this being particularly so with young metamorphosed individuals. Seizing of prey, too, is performed at lightning speed, and, if the range is a long one, the animal may jerk its whole body in the direction of the object to be seized, thus assisting the movements of its head. The Salamander is quite capable of seizing a passing 'blue-bottle' in flight, and has been observed to do so. The climbing powers of some individuals are also rather astonishing, and it has been found necessary to keep a piece of wire-gauze over the top of a glass accumulator jar some 18 inches high, which was being used as a vivarium, in order to prevent the escape of the inmates. This they attempted by climbing up the angles, chimney fashion.

The colour markings are subject to great variation within certain limits, some individuals being almost entirely yellow, while others again are nearly black. Some have thought that the intensity of colour is controllable by varying the environmental conditions, e.g. background, temperature, and humidity, and further that such adaptive changes are transmissible to future generations. This question is one of experimental zoology rather than of anatomy, and it is not proposed to discuss the matter here. The works of Kammerer,

MacBride, Knoblauch and others given in the bibliography should therefore be consulted by those interested in this subject.

VARIETIES

In spite of so much variation in the relative proportions of the yellow and black pigments, three main and fairly constant varieties stand out clearly. They are based on differences of pattern, and appear to be correlated, to a very large extent, with geographical distribution. These varieties have been carefully investigated by E. G. Boulenger (1911) and the following description is a résumé of his work (cf. Frontispiece).

1. *Forma Typica.*

The first of these varieties may be called the *forma typica*, since it is the type on which Laurenti first established the genus. In this variety the black pigment nearly always predominates over the yellow, while the latter pigment is disposed over the body as markings of various shapes, often in three or five alternating series, or with a median series forming a sinuous or zigzag vertebral stripe. Very exceptionally the dorsal markings may appear to form two longitudinal series, but in such a case they never hang together in regular chains continuous with the spots on the paratoids. The upper eyelids and paratoids are usually entirely, but sometimes only partially, yellow, and these usually remain distinct from each other, but they may fuse. A yellow spot occurs nearly constantly above the angle of the mouth, while the snout is usually entirely black. There are sometimes a few markings in the gular region, but they may be absent. The ventral surface is either quite black or marked by a few small spots. The limbs are black with a characteristic and constant yellow patch on the proximal portion of the dorsal surface of the arm and thigh, and a second similar patch may or may not occur on the distal portions of the limbs. The spots on the tail may be single or paired, or they may form a stripe. The ventral surface of the tail is nearly always black. The colour of the markings varies from chrome-yellow to deep orange.

With very few exceptions all specimens occurring to the east and south of a line drawn through the Erz mountains, the Danube, the Alps, and the Rhône belong to this form (Pl. XXV, fig. 84).

2. *Variety Molleri.*

The second form occurs in the Spanish peninsula. It is the *variety molleri* of Bedriaga (1896), and includes Seoane's *var. galliaca*

(Seoane, 1884). This might almost be described as a sub-variety of the *forma typica*, since a practically uninterrupted series can be traced between the two forms, both of which occur on the Peninsula. Two descriptions of this type may be quoted. The first, by Bedriaga, states that the colour and pattern of this variety is rather variable. The ground colour is usually greyish-brown, sometimes of a more dirty grey, sometimes more brownish-black or even black, and is broken up above and below by pale yellow spots with the addition of grey or greyish-brown spots, into which the yellow passes gradually. The yellow spots on the sides of the body, the limbs, the tail, the paratoids, the throat and on the eyelids, are as if powdered over with red dust, or washed with red, or even blood-red. The throat may sometimes be a deep red colour, and the dorsal spots show here and there a red dot. The yellow spots are very variable both in number and size. The second description by G. A. Boulenger concerns some specimens kept at the Zoological Gardens. He says that some specimens were black, variegated with various tints of grey, brown, pale yellow, and crimson. The latter colour was particularly conspicuous on the upper eyelids and the paratoid glands, the base of the limbs and the throat, but it appeared as small patches within the area of the more or less irregular pale yellow spots with grey centres which were dispersed very irregularly on the body and tail. One of the specimens was pale olive-grey above, and on the sides freckled with black and pale greenish-yellow spots, the black appearing as an irregular vertebral stripe, a dorso-lateral stripe, and bars on the flanks. The upper eyelids, the paratoids, and the throat were claret-red. The coloration of such a Salamander has a lichen-like appearance more suggestive of assimilation to surroundings than of warning to enemies. E. G. Boulenger discussing this type says:

‘On careful examination of the red and grey markings in these specimens I have come to the conclusion that these are due, not to special pigments in addition to or in combination with the yellow, as has been supposed, but to the absence of pigment, the pigmentless flesh highly flushed with blood being exposed on certain patches and the grey colour resulting from the absence of yellow combined with a small quantity of black pigment.’

Forma typica also occurs all over the Peninsula side by side with this variety.

3. Variety *Taeniata*.

The variety which is commonly imported into this country and on which the present investigation has been carried out is the *variety*

taeniata, so called on account of the arrangement of the dorsal markings in two parallel series continuous with the patches on the paratoids, which not infrequently form two uninterrupted stripes. This peculiarity distinguishes it unmistakably from the other two types. Even when the two stripes are only quite fragmentary they retain their individuality and parallel disposition, not encroaching over the mid-dorsal line except occasionally above the occiput and in the posterior region of the body, where they may be connected by cross bars. Another point of difference is that the yellow markings are usually present on the snout, while the spot situated above the angle of the mouth in *forma typica* is frequently absent in *taeniata*. On the limbs black usually predominates, and there is a similar characteristic yellow patch in each variety near the base of the arm and thigh, but the second patch on the fore-arm and leg which is variable in *forma typica* is constant in *taeniata*, and usually larger than in the typical form. Not infrequently yellow is in excess of the black and often extends to the ventral surface of the tail, which is rarely the case in the other forms.

The colour varies from sulphur- or lemon-yellow to a deep orange. Fr. von Schweitzerbarth (1909) obtained some specimens near Stuttgart with markings almost vermilion red in colour. She named them *var. coccinea* but they clearly represent only individual peculiarities. Albinism has been reported in several cases (see Schreitmüller, 1909, and Wolterstorff, 1909).

The habitat of *var. taeniata* is restricted—with the exception of one doubtful specimen from Rome—to France, Spain, Portugal, south Holland, Germany, and Switzerland (Pl. XXV, fig. 84).

Excellent accounts of the external characteristics as well as of the life-history and ecology of the Salamander have been given by Bruno Dürigen (1897) and by Schreiber (1912). The arrangement of the varieties adopted by these two authors is different in each case and also differs from that adopted here, the last-named author describing as many as thirteen varieties and sub-varieties. Such elaboration seems unnecessary, since it concerns only the relative amounts of the yellow and black pigments present and whether the spots are confluent or discrete, and so on.

BIBLIOGRAPHY OF SECTION II

30, 31, 50, 67, 73, 76, 151, 155, 197, 217, 219, 301, 312, 357, 359, 360, 362, 363, 395, 436, 468, 558, 673, 677, 683, 688, 689, 692, 693, 710, 730, 734, 776, 778, 779, 784, 821.

III

THE SKELETON

THE literature dealing with the osseous skeleton of the Salamander is very extensive, so that anything approaching a complete résumé would be too lengthy to include here; neither would any particular advantage be attained by so doing. All the chief original contributions to our knowledge of the structure and homologies of the various elements, as well as those accounts definitely needing correction, are, however, referred to in the text.

As an aid to the study of the skeleton in general, and particularly in differentiating between cartilage and bone, it is advantageous to steep the macerated and semi-cleaned bones in a saturated solution of alizarin in alcohol for a few hours. Subsequent immersion in 70 per cent. alcohol will extract the dye from the soft tissues and from the cartilage, and leave the osseous parts stained a bright magenta.

THE AXIAL SKELETON

I. THE VERTEBRAL COLUMN (PLATE III).

1. General.

The total number of vertebrae is somewhat variable, the most variable region being the tail, the average being about forty. Funk (1827) gives forty-two as a definite number, but a specimen with as few as thirty-eight has been counted, while List (1883) mentions an example having forty-three, and Hoffmann (1873-8) gives a total of forty-four. Four regions are distinguishable, namely, the *cervical* with one vertebra, the *trunk* with thirteen to fifteen, the *sacrum* with either one or two vertebrae, and the *caudal* region with some twenty-two to twenty-five. Funk further distinguishes a thoracic region, but the term 'thorax' is a misnomer when applied to an Amphibian.

2. The Cervical or Atlas vertebra.

The *Cervical* or *Atlas* vertebra (Figs. 10 and 11) differs rather widely from the general pattern. The centrum is almost non-existent, being present only at the posterior end at the articulation with the second vertebra. The neural arch is high and bears a well-formed neural spine (nl.sp.). It slopes off obliquely at the anterior end so as to leave a gap between the occipital region of the skull and the arch

of the vertebra which is closed by a strong tough membrane. The anterior end bears two large concave facets for articulation with the occipital condyles (fa.con.), while there is also a well-marked median process, the so-called *odontoid process* (pr.o.), which fits into the foramen magnum of the skull and articulates, by means of two small lateral facets, with the bony side-walls of this foramen. Each side of the neural arch is perforated by three foramina, one near the anterior end for the emergence of the first spinal nerve (fo.n.sp.I.), another near the posterior end for the second spinal nerve (fo.n.sp.II.), and the third near the middle, the *foramen nutritum* (fo.nt.), for the passage of blood-vessels. The foramen for the second spinal nerve may not always be completely surrounded by bone but may merge into the intervertebral foramen, which is normally closed by a membrane.

The homology of the first cervical vertebra of Urodeles has caused a considerable amount of discussion. The earlier workers, e.g. Hoffman, Hyrtl, Wiedersheim, &c., considered it to be of a double nature, since they regarded the 'odontoid' process as the centrum of a vertebra which possessed no neural arch, and they thought that the 'atlas' probably represented the second vertebra of Amniota. On this assumption they call the first spinal nerve N. spinalis II. Parker (1882), while agreeing as to its multiple nature, regards the vertebra as representing a portion of the occipital region of Amniota, and therefore thought that the second vertebra of Urodeles was the equivalent of the atlas of Amniotes, and with this view Stöhr (1880)¹ agrees. Albrecht (1878) supposes the vertebra to be the homologue of the pro-atlas of Reptiles, while Peter (1895) agrees with Parker and Stöhr that it corresponds to the occipital segment of higher vertebrates, but disagrees with them in that he thinks that it is a single vertebra, and not two fused together. In favour of the older view Froriep (1917), working on the development of *Salamandra atra*, claims that the first vertebra comprises vertebrae I and II and that the first spinal nerve of the adult is the morphological second, since at one stage he finds a transitory vestige of a nerve emerging between the occiput and the vertebral column. More recently still Mookerjee (1931) has reinvestigated the problem and finds that there is a pair of intercalated cartilaginous arches between the occipital arch and the atlas (first) arch proper, and further that the occipital joint arises from these arches, the cups fusing with the atlas arch and the balls with the occipital arch. He also showed that the 'odontoid' process is the intervertebral cartilage of this arch. The cups and the 'odontoid' process Mookerjee terms the pro-atlas.

¹ Stöhr deals only with Triton (*Zeitschr. f. wiss. Zool.*, Bd. 33, pp. 477-526).

To sum up then, there would seem to be some truth in each of the two earlier and apparently conflicting views, since the first vertebra of the adult *has* a double origin while a part of the intercalated arch also fuses with the skull.

3. The Trunk Vertebrae.

The *trunk vertebrae* are all essentially similar. The actual one figured (Figs. 13–17) is the last pre-sacral and may be taken as typical of the whole group. The *centrum* (cen.)—or *corpus*—is well formed and rather skittle-shaped. It is oval in cross-section and very strongly opisthocelous, the posterior concavity tending to become rather deeper towards the ventral side. The ends of the centrum remain cartilaginous, but the body is ossified and hollow, the cavity being filled with a fatty marrow. The *neural canal* (can.nl.)—or *foramen vertebrale*—is somewhat pentagonal, the *zygapophyses*—or *processi articulares*—are well formed and wing-like, especially those at the posterior end, which are very broad and form a roof over the spinal ganglia. The obliquity of the sliding surfaces is very slight. The *neural spine*—or *processus spinosus*—forms a well-defined ridge anteriorly but fades away posteriorly. The mesial portion of the neural arch between the posterior zygapophyses is thickened, and bears on its posterior surface a pair of small but well-marked depressions, one on each side of the middle line. From these concavities the *MM. interspinales* arise (see p. 93). The anterior edge of the neural arch is V-shaped, so that a triangular space exists on the dorsal side between one vertebra and the next which is closed by membrane. The *transverse processes* (pr.tr.) which are stout and very deep dorso-ventrally protrude in a postero-lateral direction and bear *ribs* (rb.).

4. The Ribs.

The question of the articulation of the Urodele rib with the transverse process, and of the homology of the ribs with those of Amniota, has long been a somewhat vexed problem, but it has recently been cleared up by Gray (1931), who worked on the development of the ribs in Triton. An examination of the adult condition only would lead one to suppose that both heads of the rib articulate with the bifid transverse process, and indeed this was the view generally held until the appearance of Gray's paper. It was supposed that the attachment of the rib to the chorda, i.e. the capitulum of the rib, was represented by a transitory vestige only, but Gray showed that the reverse is actually the case, and that the chondrification of the rib rudiment is a centripetal process, the capitular process growing inwards towards

the centrum *after* the remainder of the rib has been formed. This capitular process passes ventral to the vertebral artery, thus enclosing it in a bony canal. Hence it is apparent that the Urodele rib is strictly homologous with the Amniote structure both with regard to its insertions on the vertebra and its relation to the artery, but since the capitulum fuses with the vertebra in the adult a *secondary articulation* is formed with the transverse process, thus masking the true relations.

A detailed review of the earlier literature would be too lengthy to be included here, but the works of Göppert (1895) and Mayerhofer (1909) stand out prominently, and the latter includes a good historical review up to that date.

The ribs are better developed in the anterior region of the trunk, particularly those of the second and third vertebrae (Fig. 12), while towards the pelvic region they become reduced to mere acuminate appendages of the transverse processes. The first four or five ribs are bent more or less sharply downwards at about their middle, and from the point of bending there projects a sharp spine pointing in a postero-dorsal direction. The ribs of the second vertebra, and to some extent those of the third also, bear at their lateral extremities large spatulate expansions composed mainly of cartilage. From these expansions arise the *MM. thoraci-scapulares* suspending the scapula (see p. 74).

The spinal nerves do not emerge from the neural canal through the intervertebral foramina as is the case in most animals, but through a special foramen situated immediately posterior to the transverse process. The intervertebral foramen is nevertheless quite large, but is permanently closed by a tough fibrous membrane (mem.iv.). Murray (1897) has investigated *Spelerpes* and *Plethodon* and has come to the conclusion that the phenomenon, which is fairly general among Urodeles, does not lend support to the theory that Urodele vertebrae are double structures as had been suggested. List (1883) describes one case of abnormal fusion of the seventh and eighth trunk vertebrae of a Salamander which was so complete as to simulate a single vertebra, but they disclosed their dual nature by the fact that they each bore a pair of ribs.

5. The Sacrum.

The *sacral vertebra* is normally the sixteenth, but Claus (1876), who has made a special investigation of this region of the vertebral column, finds that either the fifteenth or the seventeenth vertebra may exceptionally articulate with the pelvic girdle, and mentions also

three asymmetrical cases in which the ilium was attached to the rib of the sixteenth vertebra on one side and of the seventeenth on the other. The vertebra itself conforms to the general pattern of the trunk vertebrae already described, but it is slightly larger and its transverse processes and ribs are very stout and long. The extremities of the ribs are pointed and not flat as are those which support the shoulder. The ilia are closely bound to them by fibrous tissue.

6. The Caudal Vertebrae.

The *caudal vertebrae* (Figs. 18 and 19) exhibit a gradual reduction in the transverse processes which, however, never entirely disappear even at the tip of the tail. The zygapophyses are also reduced in accordance with the diminishing size of the vertebrae as a whole, but they likewise are never entirely absent. As a rule only the first caudal vertebra bears ribs and they are always very small. The most noteworthy departure from the typical form exhibited by this section of the vertebral column is the possession by all but the three anterior vertebrae of a *ventral* or *haemal* arch (h.ar.), through which passes the caudal artery and vein. These arches are doubtless homologous with the chevron bones of Reptiles and some Mammals, but they are completely fused with the centra of the vertebrae. The posterior end of each haemal arch is spread out fan-wise and is slightly lipped, while the anterior end narrows considerably and is splayed off very obliquely on the ventral side so that it does not extend quite to the anterior end of the centrum on the dorsal side. There is a low crest running along the mid-ventral line, while the sides are perforated just below the transverse processes by a foramen (fo.nt.) which permits the exit and entrance of the segmental blood-vessels of the tail. The whole series forms a bony canal as complete as the neural canal, and quite unlike that formed by the slight 'Y'-shaped chevrons of the Lacertilian type found in some Urodeles, e.g. *Necturus*.

II. THE SKULL (Pls. I and II).

1. The Skull as a Whole.

One of the earliest investigators to describe the skull in any detail was Dugès (1834). His account is very condensed and is not much more than a catalogue of the several bones, but he was the first to show that the *os triangulare* is of branchial origin and has nothing to do with the shoulder girdle. Then follows Parker's well-known work (1882) in which the primordial skeleton is distinguished from

its investing bones, and some account is given of the development. There are unfortunately several inaccuracies in this work which will be referred to in detail in the subsequent description. Gaupp (1898) gives an excellent summary of the work done up to that date but adds little to it. The same author published a similar work in 1905 dealing with the development of the skull. In recent years Stadtmüller (1924) has undertaken a complete and detailed reinvestigation of the development of the skull of the Salamander, and his work has been accepted as a basis for the following investigation of the adult skull.

As an introduction to this important part of the skeleton it may be well to quote the words of William Kitchen Parker when describing the skull of *Salamandra maculosa* in 1882 (p. 172):

'The skull of the adult of this species shows at once the likeness and the unlikeness of this type to that of an average Batrachian; yet in reality this skull differs as much from that of *Rana temporaria* or of *Bufo vulgaris* as it did in its early conditions and in the mode of its metamorphosis. But scattered up and down the great Batrachian "order" there are remarkably generalized types whose skulls, now in this and now in that agree with this of the highest kind of "Caducibranchiate" Urodele. I shall, therefore, carefully set down the characteristics of this skull, and then it can be used as a measure, being "perfectissimum in suo genere", of the lowness or height, in type, of the skulls of other Urodeles, and also as a test of what is normal or aberrant in the skulls of the Batrachia. This species and *Rana temporaria*, therefore, will be taken as convenient, and yet worthy, representative Salamandrian and Batrachian types. They are culminating forms, being most perfectly specialized according to their kind.'

These sentiments may well be extended beyond the skull to the animal as a whole, for, just as the Frog is an excellent basic type of Anuran specialization, so the Salamander, considered as a whole, is one of the best examples of Urodele organization, towards which other types may be regarded as leading, or from which they may be derived.

The general outline of the skull as seen from above or below is roughly that of an equilateral triangle, of which the base-line is drawn through the quadrates. The occipital region extends only slightly behind this line. The jaws are widely spread laterally, thus giving the broad flattened appearance characteristic of Amphibia in general. The orbital rim is incomplete, since the maxilla and quadrate are connected by a jugal tendon only; there being no osseous bridge. Thus in general shape the skull of the Salamander bears fairly close resemblance to that of the Frog, but in detailed structure they differ widely.

Any description of a Urodele skull falls naturally into two clearly defined sections, first, the *primordial skeleton*, comprising both cartilage and endochondrial ossifications, and second the *investing bones*.

2. The Primordial Skeleton.

The primary cranium of the Salamander is in many respects less developed than either the Frog or Dog-fish, and forms an excellent 'ideal' type. Both the roof and the floor of the brain-case are almost uncovered, the bridges between the right and left sides being entirely confined to the regions of the sense capsules. Thus the chondro-cranium consists roughly of a pair of olfactory capsules and a pair of otic capsules connected together by two longitudinal bars of partially ossified cartilage, while with the otic capsules are associated the occipital ring posteriorly, and the palato-quadrate laterally. As a protection to the eye a sclerotic ring is developed around that organ in the larva, but disappears during metamorphosis. Four regions of the primary skull are thus distinguishable.

(a) The **Ethmoidal Region** consisting of the nasal capsules and their connectives. The accurate and detailed study of this region is practically impossible except by one or other of the reconstruction methods; any attempt to raise the investing bones being almost sure to damage the thin cartilages lying beneath. Bremer (1924)¹ adopted the wax-plate method of reconstruction and studied the development of the nasal capsules of *Salamandra* very thoroughly by this means. The following description of the ethmoidal region is based largely on his account.

This portion of the primary skeleton forms about 30 per cent. of the total length of the skull. The walls of the nasal capsules are by no means complete, but are perforated by several large fenestrae as follows:

(i) The *fenestra basalis nasi* (fen.b.nas.) in the floor is covered ventrally by the pre-vomer and, to a slight extent, by the pars palatina of the maxillary. The *internal nares* (nar.i.) or *choanae* enter the posterior portion of this fenestra. It is bounded posteriorly by the *cartilago antorbitalis* (c.a.or.), laterally by the *cartilago ectochoanalis* (c.ec.ch.), anteriorly by the *cornu trabeculae*, and mesially by the

¹ Bremer's account has not been published under his name but is incorporated in Stadtmüller's (1924) paper on the skull. By the kindness of the Librarian of the University of Göttingen the author has been enabled to consult the original typescript of Bremer's thesis.

trabecula, to which is fused the *planum internasale* (c.pl.in.)—a flat cartilaginous plate connecting the nasal capsules ventrally.

(ii) On the dorsal side of the nasal capsule is the *fenestra dorsalis nasi* (fen.d.nas.) lying opposite to the fen. basalis. The nasal, pre-frontal and frontal all assist in covering it. It is approximately quadrangular in shape and is bounded mesially by the *columella ethmoidalis* (c.col.eth.) (Higgins), or the dorsal arch of the trabecula, while postero-laterally it is bounded by the *planum conchale* (c.pl.con.), and antero-laterally by the *cart. obliqua* (c.obl.).

(iii) Two fenestrae perforate the lateral wall of the nasal capsule. The anterior and larger is the *fenestra narina* (fen.nar.) which surrounds the external narial opening and its associated muscles. It is bordered dorsally by the *cart. obliqua*, posteriorly by the *cart. retro-narina* (c.rt.nar.), and anteriorly by the *cart. cupullaris* (c.cup.).

(iv) Posterior to the fenestra narina and separated from it by the *cart. retro-narina* lies the *fenestra infra-conchalis* (fen.i.ch.) (or *lateralis*, Bruner). This opening lies at the extreme postero-lateral angle of the nasal capsule and is considerably smaller than the others already described.

(v) The *fenestra olfactoria* (fen.ol.) penetrates the nasal capsule from the cranial cavity and serves for the passage of the olfactory nerves.

The *cartilago antorbitalis* (c.a.or.) which separates the nasal capsule from the orbit is perforated by a pair of foramina, the *for. orbito-nasale laterale* (fo.o-nas.l.) and *mediale* (fo.o-nas.m.), through which pass the terminal rami of N. ophthalmicus profundus V.

Thus the primary olfactory capsules of the adult Salamander consist of a series of cartilaginous bridges, while the intervening spaces are roofed over by the investing bones of the secondary skeleton. In addition to the cartilages already named in connexion with the fenestrae there are the following small projections. From the *cart. ectochoanalis* is a small backwardly projecting process which Seydel calls the *Gaumenfortsatz* (pr.S.). From the anterior end of each nasal capsule a small cartilaginous horn protrudes antero-mesially. This is the *processus prenasalis inferior lateralis* (pr.nas.) and represents the remains of the cornu trabeculae. Just below this process is a small opening for the exit of a nerve. It is the *foramen apicale*, and, according to Bremer, it is not entirely constant.

The olfactory capsules of either side are connected together ventrally by a flat plate of cartilage which projects backwards under the anterior end of the brain, and extends forwards to about the centre of the ethmoidal region. It is the *planum internasale* (c.pl.in.). The

anterior portion of the space between the nasal capsules is thus open ventrally. It is called the *cavum internasale* (ca.in.) and houses the intermaxillary gland. The posterior wall of the *cavum internasale* is formed by the *septum internasale*, which connects the nasal capsules posteriorly. It forms the cartilaginous partition between the *cavum cranii* and the *cavum internasale* and bounds the mesial borders of the *fenestrae olfactoriae*. The *tectum internasale* (c.t.in.) unites the capsules dorsally and thus forms a roof to the *cavum internasale*. It is prolonged anteriorly in the middle line to a short beak, the *rostrum prenasale* (Parker) (c.r.).

(b) The next region of the primary skull is the **Orbito-temporal**. It consists of a pair of vertical lamellae joining the olfactory capsules to the otic capsules, and forming the sides of the brain-case, so that they separate the *cavum cranii* from the orbits. They are perforated by two foramina of which the larger is the *for. opticum* (fo.op.) and the other, immediately posterior to it, is the *for. oculomotorium* (fo.oc.). The optic foramen would perhaps be better termed the *optic fenestra*, since its diameter is much greater than the optic nerve, and it is largely closed by membrane. In the adult the part of each lamella anterior to the vertical diameter of the *for. oculomotorium* becomes ossified, and the resulting bone is most usually termed the *orbito-sphenoid* (o.o-s.), although Broom holds that it is the homologue of the Mammalian *pre-sphenoid* and Noble refers to it as the *sphenethmoid*. The older and more widely used name is retained here.

(c) The **Otic Capsules**. The membranous labyrinth of the auditory capsule is entirely enclosed by the primary skeleton which, in the adult, ossifies completely with the exception of the operculum. The capsules are relatively large and somewhat flattened dorso-ventrally, especially towards the posterior region. On the dorsal surface may be seen the convex ridges marking the position of the semicircular canals of the labyrinth. The lateral end of the ridge covering the horizontal canal is somewhat roughened where it meets the squamosal and it is often referred to as the *crista muscularis* (cr.m.) from the fact that certain spino-occipital muscles are attached thereto. The ventral and anterior surfaces of the capsule are much smoother. On the postero-lateral face, and directed somewhat ventrally, is an oval opening in the capsule—the *fenestra vestibuli*. The fenestra is closed by a tough fibrous membrane, to the outer surface of which is attached the *operculum* (c.op.). The *operculum* is a heavy plate of cartilage, strongly convex on its external surface and slightly concave internally, so that in transverse section it appears as a thick crescent. The M. opercularis attaches this element to the suprascapula. The

probable function and *modus operandi* of these structures are discussed on p. 295.

The lateral wall of the capsule is attached at three points to the suspensorium (palato-quadrate), and the details of this attachment will be considered in dealing with that part of the skull. The mesial wall of the otic capsule, separating the labyrinth from the cavum cranii, is perforated by five foramina, namely, the *for. perilymphaticum* (fo.pl.), the *for. endolymphaticum* (fo.el.), and three *for. acustica* (fo.au.).

The *for. perilymphaticum* (fo.pl.), through which the duct of the same name passes into the cavum cranii from the labyrinth, is situated close to the base of the capsule, towards the posterior end.

The *for. endolymphaticum* (fo.el.) serves a similar purpose for the ductus endolymphaticus and lies a little anterior to the former—at about the middle of the capsule—near the *dorsal* wall.

The three *for. acustica* (fo.au.) in the adult lie almost in the floor of the capsule rather than in the mesial wall, owing to growth changes in that region. They serve for the entry of the auditory nerve and hence correspond to its three rami. They lie very close together and immediately anterior to the *for. perilymphaticum*.

The cavity of the capsule is not quite simple but is subdivided by bridges which develop around the semicircular canals, the *septa semicircularia* (Stadtmüller). The *septum semicircularium anterior*, passing from the antero-mesial to the dorsal wall, is very well developed, while the *sept. semicirc. laterale* is considerably weaker and is not always complete. The *sept. semicirc. posterior* is usually only faintly indicated and never develops completely.

The otic capsules are completely fused to the cranium and ample traces remain of the parachordal plate. In the occipital region the capsules are joined together by a broad *hypochordal commissure* (c.hyp.com.), and, at their anterior ends, by a narrow bar of cartilage, the *crista retrosellaris* (c.cr.rs.) (Stadtmüller). Between the two bridges the parachordals are represented only by slight ridges along the ventro-mesial borders of the capsules. The auditory capsules are also joined together dorsally by a narrow commissure at the posterior end, the *tectum synoticum* (c.t.syn.). There are thus two fenestrae in the floor of the primary cranium, an anterior and a posterior. The *fenestra basicranialis anterior* (fen.bc.a.) is the larger and is bounded anteriorly by the planum internasale, laterally by the orbito-sphenoids (representing the trabeculae), and posteriorly by the crista retrosellaris. The *fenestra basicranialis posterior* (fen.bc.p.) lies between the crista retrosellaris anteriorly and the hypochordal commissure posteriorly, and is bounded laterally by the remains of the parachordal

plate. Both fenestrae are of course covered in the adult skull by the parasphenoid bone. Practically the whole of the ear capsule except the operculum ossifies in the mature adult, although the rim of the fenestra vestibuli and the inner surfaces bounding the cavum vestibuli tend to retain their cartilaginous nature. The combined glossopharyngeus-vagus nerve passes through the *foramen post-oticum* (fo.p.ot.) between the ear capsule and the occipital segment.

The occipital ring remains almost entirely cartilaginous, and it is only the deeper parts of the condyles which ossify and fuse with the ear capsules. The composite ossification thus formed is best called the *occipito-petrosal* (Stadtmüller).

(d) The **Palato-quadrate** (c.p-q.). The suspensorium is attached to the lateral aspect of the ear capsules by three processes, tripod-like, so that a cavity with three exits is enclosed between the palato-quadrate and the capsule. This cavity is the *antrum petrosum laterale* (Drüner), and through it pass the Art. and Vena petrosa lateralis and the facial nerve.

Of the three attaching processes the *processus ascendens* (pr.asc.) is the smallest. It is continuous with the lateral skull wall and separates the N. ophthalmicus profundus V from other two trigeminus branches. It also separates the artery from the vein. Normally the process remains unossified, but in old animals a certain amount of perichondrial ossification may occur. The *processus oticus* (pr.ot.) (proc. lateralis dorsalis, Drüner) is the dorsal process and lies beneath the squamosal. It is rather larger than the proc. ascendens, but, when compared with the larval condition, it shows a tendency to lose its connexion with the ear capsule through the ingrowth of connective tissue (Stadtmüller, 1924). It remains cartilaginous. The *processus basalis* (pr.ba.) (proc. lateralis ventralis, Drüner) is by far the largest of the three, and, as its name suggests, lies ventrally directly opposite the proc. oticus. According to Stadtmüller it first fuses completely with the larval skull and then separates from it again by the ingrowth of connective tissue, but this secondary segmentation occurs a little lateral to the point of the original fusion, so that a portion of the primitive proc. basalis is left fused to the capsule and forms the base of the canal through which the facial nerve emerges—the *facialis canal*. The now secondary *proc. basalis*—which is the only part recognizable in the adult—is thus separated from the primary portion by connective tissue, and the most convenient way to dissect the antrum petrosum laterale, in order to examine its contents, is to disarticulate this junction from the ventral side, when the whole suspensorium may be turned back, and, after breaking through the

other two processes, removed entire. The *quadrate* (o.qu.) forms the direct lateral continuation of the basal process and points almost at right angles to the skull axis in an obliquely downward direction. It articulates directly with the lower jaw and always ossifies to a greater or lesser extent, being in fact the only portion of the suspensorium to do so normally. The *processus pterygoideus*, or 'cartilaginous pterygoid' (c.pt.), arises from an independent chondrification in the 35 mm. larva (Stadtmüller) but is continuous with the palato-quadrate in the adult, from which it protrudes antero-laterally towards the posterior end of the maxilla, pointing somewhat obliquely downwards. It is only a narrow rod of cartilage and lies in a groove in the osseus pterygoid (which belongs to the investing bones of the skull) and usually protrudes a short distance anterior to it.

The suspensorium is attached to the maxilla by two ligaments, the *jugal ligaments*, namely *lig. quadrato-maxillaris externum* and the *lig. quadrato-maxillaris internum*, which pass laterally and mesially of the M. levator mandibulae respectively.

3. The Investing Bones.

In contrast with the slow and tardy ossification of the replacing bones the investing bones arise very early, and are already well formed at birth, so that it is advisable to treat any larva with either a decalcifying fluid or an acid fixative before attempting to section it. Nevertheless they always remain thin and leaf-like. The following bones are present: on the dorsal side, *pre-maxilla*, *maxilla*, *nasal*, *frontal*, *pre-frontal*, *parietal*, *squamosal*—all are paired. On the ventral side there is an unpaired median *parasphenoid* and paired *pre-vomers* and *pterygoids*, while both the *pre-maxillae* and *maxillae* have palatine processes. According to Stadtmüller a *quadrato-jugal* occurs, appearing first in a larva of 27 mm., but it always remains small and, in the adult, fuses homocontinuously with the palato-quadrate so as to be indistinguishable.

The *pre-maxillae* (o.p.m.) are paired in the Salamander and form the skeleton of the snout. They are sometimes called *intermaxillaries* (Funk, Bolkay). Three regions are distinguishable in each bone which, according to Stadtmüller, arise as three distinct ossifications. These are: (a) the *pars prenasalis* (or *dorsalis*) which ascends over the dorsal side of the nasal capsule and ends in a sharp slender process which to some extent overlaps the nasal and frontal. (b) The *pars dentalis* forms the anterior border of the upper jaw and bears teeth—it is in fact formed by the fusion of tooth sockets. It is joined to the *pars prenasalis* dorsally and to the *pars palatina* postero-mesially.



(c) The *pars palatina* is a narrow but strong bar of bone which helps to form the osseous palate. According to Stadtmüller it arises partly by the fusion of tooth sockets and partly as a separate ossification direct from the membrane.

The *maxillae* (o.m.) complete the arch of the upper jaw and surround the latero-ventral edge of the cartilaginous nasal capsule like a gutter. Like the pre-maxillae each bone has three parts: (a) The *pars facialis* borders the postero-lateral margin of the external nasal aperture and covers the side of the face as far as the antero-lateral angle of the orbit. Dorsally it extends on to the edge of the nasal, and ventrally it fuses with (b) the *pars dentalis* which, like the corresponding part of the pre-maxilla, arises by the fusion of tooth-sockets. The teeth only extend backwards to about the level of the anterior margin of the optic fenestra. (c) The *pars palatina* corresponds entirely with the similarly named portion of the pre-maxilla, against which it abuts anteriorly. On the mesial side it meets the pre-vomer. The maxilla extends posteriorly to about the level of the hinder border of the optic fenestra. Its posterior extremity lies lateral, and slightly caudal, to the anterior extremity of the pterygoid, and is joined to the lateral extremity of the suspensorium by a pair of tough ligaments—the *jugal ligaments*—but there is no bony connexion as in the Frog.

The *nasals* (o.nas.) are paired bones of a rather irregular shape serving to roof over the mesial portion of the nasal capsules. Their antero-lateral edges curve round the mesial border of the external nasal aperture.¹ Mesially they meet, and overlie, the antero-lateral edges of the frontals and the pre-nasal processes of the pre-maxillae, while posteriorly they adjoin the pre-frontals, and laterally meet the dorsal edges of the facial portions of the maxillae, and are slightly covered by them. The nasals are distinctly lateral in position and are widely separated from one another in the middle line. They are perforated by a variable number of foramina for the passage of the ultimate twigs of the mesial branch of the N. ophthalmicus profundus V. According to Stadtmüller their development is relatively late.

The *pre-frontals* (o.p-fr.) (*fronto-lacrymaux*, Dugès; *ectethmoid* Parker) are also paired and occur on each side of the skull immediately anterior to the orbit. They are more or less quadrangular in shape, and are comparatively small. Their anterior borders are covered by the nasals, mesially they overlie the edges of the frontals, while laterally they are in turn pushed under the dorsal edges of the facial

¹ It should be noted that the aperture formed by the edges of the pre-maxillary, maxillary, and nasal bones is larger than the actual cutaneous opening.

portions of the maxillae. The posterior edge of the pre-frontal is free and forms a bony rim to the antero-dorsal border of the orbit. The *ductus naso-lacrimalis* (d.nas-lc.) enters a foramen at the postero-lateral angle of the bone, and passes antero-lateralwards under it and the pars facialis of the maxilla to enter the nasal capsule near the external narial opening.

W. K. Parker (1882) describes and figures a septo-maxillary at the antero-lateral angle of the apertura nasalis externa, between the maxilla and the pre-maxilla, but he is the only author to do so. Stadtmüller (1924) declares himself totally unable to find it in any of his sections, and Lapage (1928) also failed to detect any such bone. Bruner (1902) describes the bone in certain other Urodeles but says it is wanting in Salamandra. The present investigation confirms the result of the later workers. It therefore seems that Parker must have been mistaken or that he encountered a very abnormal specimen. In view of Lapage's work the latter alternative is unlikely.

The brain-case proper is roofed over by two pairs of investing bones, namely the frontals and parietals; they remain separate throughout life and do not fuse as in the Frog.

The *frontals* (o.fr.) are large and extend far forwards under the prenasal processes of the pre-maxillae, while their antero-lateral borders also underlie the nasals for some distance and meet the mesial edges of the pre-frontals. The lateral edge of each frontal turns down ventrally and meets the orbito-sphenoid, while posteriorly the frontals overlap the anterior edges of the parietals. The sagittal suture is very irregular and is by no means a straight line. There is no post-orbital process as in some Urodeles.

The *parietals* (o.par.) lie immediately posterior to the frontals and have approximately the same superficial area. They complete the roof of the cranial cavity, while their posterior ends spread out laterally over the mesial portions of the ear capsules. N. trochlearis may penetrate the parietal, but, in older animals at least, this nerve usually passes through a foramen in the orbito-sphenoid. The parietals do not extend quite to the dorsal rim of the foramen magnum but leave a portion of the *tectum synoticum* exposed. The dorsal surface of the frontals and parietals is very flat, or even slightly concave as seen in transverse section, and while both are relatively thick bones they are very transparent, so that it is quite easy to distinguish the main features of the brain through them, even in the adult.

The *squamosals* (o.sq.) (*tympanicum*, Wiedersheim; *paraquadrata*, Gaupp) are paired splint-like bones lying on the dorsal side of the quadrates, to which they become very closely fixed. Each

squamosal extends from the quadrato-mandibular joint along the *processus oticus* of the palato-quadrato and becomes more or less fused with the periotic bone above the horizontal canal. While there is a distinct tendency for the bone to be 'T'-shaped it is not so definite as in the Frog.

A *quadrato-jugal* has been described by Stadtmüller. According to him it appears first in a larva of about 27 mm. and always remains small. In the adult it fuses homocontinuously with the ossified portion of the quadrato, from which it becomes indistinguishable.

The investing bones of the ventral surface are the *parasphenoid*, the *pre-vomers*, and the *pterygoids*.

The *parasphenoid* (*sphenoid*, Dugès; *Keilbein*, Hoffmann; *vomer*, in part, Broom; *vomer* + *pterygoids*, Kesteven). This bone is the largest in the skull and is characteristic of Amphibia. It forms at one and the same time a bony floor to the *cavum cranii* and a roof to the mouth, and is the only median bone in the skull. Posteriorly it extends for some distance under the ear capsules on either side, but hardly so far, comparatively, as in the Frog. In the orbital region the edges turn upwards to meet the orbito-sphenoid, so that the bone becomes gutter-shaped in cross-section. The internal carotid artery passes into the cranial cavity through a canal—the *carotid canal* (*can.car.*)—between the parasphenoid and the otic capsule.

Until quite recent years the parasphenoid has been looked upon as a typically amphibian bone, which was also present in Reptiles, but in a very reduced state. Recently, however, Broom has sought to identify the anterior part of the amphibian, and the whole of the reptilian, parasphenoid with the mammalian *vomer*, while Kesteven (1916 and 1926) claims that the posterior part of the amphibian parasphenoid is represented in Reptiles and Mammals by the *pterygoids*. Both these authors base their views mainly upon palaeontological evidence.

The *pre-vomers* (o.p.v.) (Broom) are perhaps better known as the vomero-palatines, but, if one accepts the above-mentioned conclusions with regard to the homology of the mammalian vomer, the bones now to be described can be none other than the pre-vomers. Whether any palatine element is represented will be considered later. The paired pre-vomers form a bony floor to the nasal capsules. Each bone articulates with the pre-maxilla and maxilla laterally, while mesially its anterior border bounds the large internasal space, behind which it is approximated to its fellow on the other side for a short distance. The edge of the bone then diverges from the middle line and follows the curve of the dentigerous portion. The bone also surrounds the

anterior rim of the internal narial opening and a part of the orbit. It carries a very characteristic S-shaped denticerous ridge which extends far backwards in the mouth and turns lateralwards under the ear capsule. This posterior extension is quite free from the overlying part of the skull (parasphenoid), and is separated from it by soft tissues, including the M. retractor bulbi, which passes dorsal to the posterior end. The pattern of this dentition is of taxonomic importance (cf. p. 1).

As already suggested, the older workers, e.g. Parker and Wiedersheim, regarded it as representing both the vomer and the palatine elements fused together, and named it accordingly *vomero-palatine*. In 1910 Wintrebert, as the result of an investigation of the metamorphosing skull, came to the conclusion that the palatine entirely aborts during the change from larval to adult life, and that the bone under consideration should therefore be regarded as the *vomer*. In 1924 Stadtmüller, whose careful and detailed work on the development of the skull has already been mentioned, declares that in all his examples the vomer appears to fuse with the palatine, but that it is extremely difficult to decide whether this is really the case, or whether the latter is entirely resorbed, as Wintrebert claims. He criticizes Wintrebert's work on account of the absence of any figures, details of methods, and size of the larvae investigated, and says that he prefers to agree with the older investigators. He nevertheless confirms Wintrebert's statement that the vomerine part has a double origin, while he does not discuss the possibility of an homology with the pre-vomer. He had not seen Wintrebert's chief paper (1922) against which his criticism certainly could not be levelled.

The whole question therefore remains *sub judice* and its solution lies outside the scope of the present work, but in view of the evidence of palaeontology the newer terminology has been adopted here.

The *pterygoids* (o.pt.) are a pair of more or less ploughshare-shaped bones investing the pterygoid cartilages of the primary cranium, the cartilages lying in a groove on the dorsal surface of each investing bone. The posterior end of the bone lies under the quadrate, and extends laterally almost to the jaw articulation and mesially over the *processus basalis*. The anterior extremity points antero-laterally towards the posterior extremity of the maxilla but does not quite meet it, and hence the bone forms the posterior margin of the orbit.

Kesteven identifies this bone with the reptilian *ectopterygoid* or *os transversum* rather than with the reptilian and mammalian pterygoid,

which, as already mentioned, he considers homologous with the posterior portion of the amphibian parasphenoid.¹

SUMMARY.

Reviewing then the skull as a whole, particularly in comparison with that of the Frog, the following important differences may be noticed.

- (i) The *skull generally* is more compactly built than in the Frog.
- (ii) The *nasal capsules* are more completely roofed over, since the nasals are pushed forwards by the pre-frontals, which are not present in the Frog.
- (iii) The *pre-vomers* have a much greater expansion and thus form a complete bony floor to the nasal capsules, while their dentigerous portions extend far back into the mouth.
- (iv) The *frontals* and *parietals* remain distinct elements and do not fuse as in the Frog, neither do they extend so far ventrally round the sides of the brain case.
- (v) The *brain-case* is relatively wider in *Salamandra* than in *Rana*, when compared with the width of the skull as a whole.
- (vi) The feature just noticed is due largely to the much greater development of the *suspensorium* in the Frog. In *Salamandra* the *squamosals* are mere splints on the dorsal surfaces of the palato-quadrates, while the quadrato-jugal sends no process to meet the maxilla. The pterygoid likewise does not join the maxilla so that the arch of the upper jaw is incomplete.
- (vii) On the ventral surface the *parasphenoid* is relatively broader in *Salamandra*, so that the sides of the brain-case—orbito-sphenoids—are more nearly vertical.
- (viii) The anterior rim of the *orbit* on the ventral side is formed by the edge of the pre-vomer in *Salamandra*, and by the palatines in *Rana*, the latter elements being probably absent in the adult Salamander.
- (ix) In the *ear capsule* the *columella auris* is vestigial in *Salamandra*, its place being taken by the cartilaginous *operculum*, which has no direct connexion with the skin, while in *Rana* the columella is attached to the tympanic membrane and there is no operculum.

III. THE VISCERAL ARCHES.

1. The Mandibular (First Visceral) Arch. (Pl. II, fig. 7, and Pl. III, figs. 8 and 9.)

The shape of the lower jaw as a whole is a simple bony arch, almost semicircular in plan. At the median symphysis there is a

¹ See also Watson's criticism of this hypothesis, *Journ. Anat. London*, vol. liii, pp. 239-40.

prominent *posterior mental process*. The anterior two-thirds of each ramus bears a single row of functional teeth, mesial to which a row of reserve teeth can be demonstrated in transverse sections. (For details of the teeth, see p. 262.)

The structure of the mandible, in both the larva and adult, has been thoroughly investigated by Gaupp (1911) and Stadtmüller (1924). Both accounts are in agreement and correct that of Parker (1882) by showing that the *splénial* (Operculare of the German authors) is present in the larva only, and is resorbed entirely in the adult. There are therefore two investing bones only in the lower jaw, namely, a *dentary* and a *pre-articular* (Goniale), while two replacing ossifications also occur in the persisting Meckel's cartilage, viz. the *articular* at the proximal end and the *mento-Meckelian* at the symphysis.

Meckel's cartilage (c.M.) persists as the primary skeleton of the lower jaw throughout life, and is unossified in the major part. It remains exposed at the proximal end between the two investing bones—dentary and pre-articular, while the anterior end tapers to a point and terminates a short distance from the middle line, its mesial extremity having become ossified as a *mento-Meckelian* (Mento-mandibulare, Stadtmüller), so that the median symphysis is solid bone. This ossification occurs quite late, well after metamorphosis, and becomes fused homoecontinuously with the dentary, which is probably the reason that lead W. K. Parker to say (p. 177) 'the Salamander has no mento-Meckelian bone'. The extreme proximal end of Meckel's cartilage is the only element of the lower jaw to come into contact with the suspensorium. Of this the actual surface remains cartilaginous, but the deeper portions become transformed into a small bony knob, the *articular* (o.art.). According to Stadtmüller this ossification also occurs very late and is first discernible in a metamorphosed individual of about 4.3 mm. long.

Investing Bones. The *dentary* (o.den.) forms the principal element of the adult mandible. It covers almost the whole of Meckel's cartilage laterally and most of its dorsal and ventral surfaces, and bears teeth (see p. 263). In transverse section it is more or less C-shaped, with the opening of the 'C' towards the mesial side. Anteriorly it forms an almost complete circle around Meckel's cartilage, but it opens out posteriorly and tapers at the same time, so that it terminates a little anterior to the articulation as a thin lath on the lateral aspect of Meckel's cartilage. Its fusion with the mento-Meckelian has already been mentioned. W. K. Parker describes its dorso-mesial portion as a separate element, the *splénial*, but according to

Stadtmüller, the dentary, during its development, grows round and envelops the larval splenial, which is eventually resorbed, although he thinks that a few of its anterior teeth may occasionally remain fused with the dentary. Thus the bone as above described is equal to the dentary and splenial of Parker's account. Enclosed between the dentary and Meckel's cartilage are branches of nerves V and VII, and the blood-vessels for the nutrition of the teeth, lower lip, &c.

The *pre-articular* (o.p-art.) is a wedge-shaped splint of bone which is pushed in between the free edges of the dentary on the mesial side of the jaw. It expands dorsally into a fairly pronounced coronoid process which is inflected mesially, and thus turns away from the dentary so as to expose Meckel's cartilage and the articular dorsally. It does not become fused with the articular as it does in some forms (e.g. *Triton*, Gaupp), and is perforated near its posterior end by a foramen for the R. alveolaris of N. VII and the alveolar artery (fo.i.den.). This element represents the *articular* of Parker, and is called the *Goniale* by Gaupp, Stadtmüller, and most German authors.

The Hyobranchial Skeleton. (Pl. II, fig. 6 and Pl. VI, fig. 38.) In the larval Salamander the hyoid and portions of four branchial arches are all present. In the adult, however, only portions of the hyoid and the first two branchial arches normally persist, the remainder disappearing during metamorphosis. The whole skeleton is cartilaginous with the exception of the small *os triangulare* (q.v.).

2. The Hyoid (Second Visceral) Arch.

This arch consists, in the adult, of two elements on either side, namely the *hypo-* and *cerato-hyals*. In the larva these two articulate with one another, but in the adult they become separated. The *hypo-hyals* (c.h.hy.) retain their connexion with the median longitudinal portion of the hyo-branchial apparatus, namely the *copula* (c.cop.) (or *basibranchial*, Wiedersheim), from which they protrude as a pair of short horns pointing in an antero-dorso-lateral direction, being more or less embedded in the substance of the tongue. They are often referred to as the anterior radials of the copula (see below). The *cerato-hyals* (c.c.hy.) form the anterior cornua of the hyoid. Their anterior ends are greatly expanded into broad spatulate sheets of cartilage which underlie the hypo-hyals ventrally, and also overlap one another in the middle line. Their posterior ends are much narrower and more rounded in section, and curve dorsalwards to about the level of the jaw suspension, where they are attached to the quadrate by a strong elastic ligament, the *ligamentum hyo-quadratum*.

Their posterior ends give origin to the M. sub-hyoideus, while the anterior ends serve for the insertion of M. subarcualis rectus 1.

3. The First Branchial (Third Visceral) Arch.

This consists of a narrower arcuate bar articulating with the copula on either side and comprising hypo- and cerato-branchial elements fused together homocontinuously (i.e. without interruption). Each bar is a flat oval in cross-section and its posterior end curves dorsally approximately parallel with the cerato-hyal, thus forming the posterior cornu of the hyoid. From the posterior end of this cartilage the M. subarcualis rectus 1 takes its origin.

4. The Second Branchial (Fourth Visceral) Arch.

The *second branchial (fourth visceral) arch* of the adult is represented only by the paired hypo-branchial elements (c.h.br.II.). These are slender curved bars articulating mesially with the posterior end of the copula, and fusing laterally with the previous arch at a point about two-thirds along its length. The space between the two arches is covered by a tough membrane, the *membrana intercartilaginea* (Drüner) (me.i.c.), except over the mesial third, where the membrane is incomplete to allow for the passage of the M. rectus cervicis profundus.

5. The Copula.

The *copula* (c.cop.) is the median cartilage with which those of the visceral arches articulate. It probably represents the fused basi-branchials, but it never shows signs of segmentation even in the larva. Its anterior end bears two pairs of small horn-like processes—the *radials*. As already indicated the anterior pair (c.h.hy.) of the latter are the hypo-hyals, but the posterior pair (c.rad.) have been shown by Drüner (1901) to arise secondarily during metamorphosis, and are therefore not strictly a part of the visceral skeleton. They, like the hypo-hyals, serve to attach the copula to the tongue.

6. The Os Triangulare.

The *os triangulare* (o.t.) is a small, broadly triangular bar of bone lying across the ventral side of the pharynx in an *inscriptio tendinea* at the junction of the M. genio-hyoideus and M. rectus cervicis superficialis. It is the only portion of the hyo-branchial skeleton to ossify. It represents the expanded end of the uro-branchial, and, in the larva, it is connected with the copula by a longitudinal rod which disappears during metamorphosis, although very occasionally small

vestiges may persist as little cartilaginous knobs between the right and left portions of the M. genio-hyoideus.

The chief abnormality met with in the visceral skeleton is the occurrence of a rudiment of a hypo-branchial¹ element in the third branchial (fifth visceral) arch. Four instances of such a condition occurring in larvae have been reported, namely, one case of a rudiment occurring on the *left* side (Kallius, 1901), two instances of a rudiment of the *right* side (Drüner, 1901), while Helena Tarapini (1909) finds in a 30 mm. larva of *Salamandra atra* a *pair* of small cartilages which she regards as rudimentary third hypo-branchials. During the present investigation one case has been found in which cartilages apparently representing these elements occurred in the *adult*. This has been fully described elsewhere (Francis, 1931). Drüner also reports cases where very small vestiges of the cerato-branchials III and IV have been found in the adult, and, as mentioned above, small traces of the uro-branchial shaft have occasionally been noticed.

The visceral skeleton of *Salamandra*, both larval and adult, has received a considerable amount of attention from time to time, and its several parts have been given names indicative of widely varying interpretations of their homology (a list of the more important synonyms is appended below). Rusconi (1854) was one of the first to undertake a detailed investigation of this region in the larva as well as in the adult, and his classic account of the metamorphosis of both skeleton and muscles remained without any substantial addition until 1901, when Drüner, applying more modern methods, reinvestigated the whole problem. Rusconi was of the opinion that *both* pairs of radials were of secondary origin, while Walter (1887) considered that they represented two pairs of hypo-hyals. Drüner, however, showed that the anterior pair only belong to the hyoid arch while the posterior pair are new structures. Wilder, Drüner, and others also include the laryngeal cartilages in the visceral skeleton, but Edgeworth (1920) has shown this to be erroneous (see also under 'Larynx', p. 272).

SYNONYMS OF THE VISCERAL SKELETON.

Cerato-hyal = Stylo-hyal, Dugès (1834).

Both branchial arches together = Corne thyroïdienne, Dugès.

Hypo-branchials = Kerato-branchials, Wiedersheim.

Cerato-branchials = Epi-branchials, Wiedersheim.

¹ It should be noted that only the cerato-branchial element is normally present in the larval Salamander.

Hypo-branchial I + Cerato-branchial I = Epi-branchial I, Parker.

Hypo-branchial II = Cerato-branchial II, Parker.

Copula = Basi-hyal, Dugès; Basi-branchial I, Wiedersheim, Parker.

Radials = Corne styloïdienne, Dugès; Kleine Hörner, Wiedersheim.

Anterior pair only = Hypo-hyal, Parker.

Posterior „ = Cerato-branchial I, Parker.

Os Triangulare = Os thyroideum, v. Siebold, Dugès, Walter, Wiedersheim.

= Sternum, Funk.

= Basi-branchial II, Parker.

= Os triquetum, Drüner.

THE APPENDICULAR SKELETON

I. THE PECTORAL GIRDLE AND FORE-LIMB. (Pl. IV and Pl. VII, figs. 39-42.)

1. The Pectoral Girdle. (Figs. 20 and 21.)

Each half of the shoulder-girdle of the Salamander is best regarded as a single skeletal element which is incompletely divided into three regions, rather than as an aggregate of three fused elements. The major portion remains cartilaginous, the only bone present being in the neighbourhood of the glenoid cavity.

The *glenoid cavity* (gl.) is ovoid in shape, and is guarded by prominent faceted lips on the pro-coracoid and coracoid borders. Its periphery is largely ossified except at the post-axial border.

(a) The Scapular region (Engler, 1929).

Scapula et adscapulum	Dugès (1834).
pars Scapularis	Stannius (1854-6).
Scapula et suprascapulare	Gegenbaur (1865); Wiedersheim (1892).
Scapula et suprascapulare	Parker (1868); Hoffmann (1873-8).
Scapulum et episcapulum	Sabatier (1880).
Scapulum	Perrin (1899, &c.).

The scapular region forms the dorso-lateral portion of the girdle and comprises first a proximal osseous portion which is the *scapula* proper (o.sc.), and secondly a distal cartilaginous plate forming the *supra-scapula* (c.s.sc.). The whole structure is fan-shaped and is curved in a dorso-ventral direction, so that the convexity is outwards. The scapula is elliptical in section and expands only slightly towards its distal border, where it merges into the *supra-scapula*. This latter portion expands into a broad fan, comparatively thick at its ventral border, but thinning out very considerably dorsally. It is attached to the axial skeleton by the MM. thoraci-scapularis and opercularis, as well as by connective tissue which extends over the M. dorsalis trunci to the neural spines of the second and third vertebrae. The scapula

ossifies earlier than the bony region of the ventral portions.¹ Its anterior border fuses to a considerable extent with the bony portion of the pro-coracoid, but its posterior edge only just meets the coracoid at the edge of the glenoid cavity. The angle between the anterior edge of the scapula and the lateral edge of the pro-coracoid is nearly a right angle.

(b) **The Pro-coracoid region** (c.pr.cor.).

Clavicle ou fourchette	Dugès (1834).
Pars acromialis (of scapula)	Stannius (1854-6).
Procoracoid	.	Gegenbaur (1865);	Parker (1868);	Fürbringer (1873);	
		Engler (1929).			
Précoracoïde et épiprécoracoïde	Sabatier (1880).
Clavicula	Wiedersheim (1892).
Together with coracoid portion =					
Sternum	Funk (1827).
Coracoïde	Perrin (1899).

This region of the pectoral girdle forms the anterior part of the ventral plate. It projects almost directly anteriorly from the glenoid cavity, and extends nearly as far forwards as the level of the os triangulare on the floor of the pharynx. It is spatulate in shape and slightly dished, with the convexity ventralwards. It is ossified in the region of the glenoid cavity but remains cartilaginous anteriorly, and is only imperfectly demarcated from the coracoid portion by a deep notch—the *incisura coracoidea* (in.cor.)—which separates the cartilaginous portions of the two regions. The osseous part of the pro-coracoid is entirely continuous with that of the coracoid except for the *foramen supracoracoideum* (fo.s.cor.), through which passes the N. supracoracoideus and the corresponding artery and vein. A line drawn from the glenoid cavity through this foramen to the centre of the *incisura coracoidea* may be taken to represent the boundary between the pro-coracoid and coracoid portions, which may thus be regarded as in an incipient state of separation. The free edges of the cartilage are exceedingly thin. The pro-coracoid forms a prominent lip over the anterior face of the glenoid cavity which presents a definite facet to the head of the humerus. The free edge of this lip is cartilaginous.

(c) **The Coracoid Region** (c.cor.).

Coracoïdien	Dugès (1834).
Coracoid	Gegenbaur (1865); Fürbringer (1873);
					Wiedersheim (1892); Engler (1929).
Coracoid and epicoracoid	Parker (1868); Sabatier (1880).

¹ Cf. Parker (1868); Perrin (1899); and Engler (1929).

Together with the pro-coracoid region =

Sternum	Funk (1827).
Coracoïde	Perrin (1899).

This is by far the largest portion of the pectoral girdle and extends mesially from the glenoid cavity across about two-thirds the width of the body, so that there is an overlapping of the right and left sides. It is apparently immaterial in *Salamandra maculosa* whether the right is ventral to the left or vice versa, since both arrangements are found to occur with about equal frequency, although in Triton and *S. atra* the former appears to be the more frequent condition. In *maculosa* the controlling factor is probably mechanical pressure during intra-uterine life.¹ The coracoid portion forms a more or less semicircular plate, deeply hollowed, with its convex surface ventral. Only a very small portion, in the region of the glenoid cavity, is ossified. The remainder is cartilaginous. Like the pro-coracoid its free edges are exceedingly thin, while the postero-mesial edges are attached by connective tissue to the sternal plate (q.v.). It also forms a faceted lip to the posterior border of the glenoid cavity which is entirely cartilaginous but is not so pronounced as that formed by the pro-coracoid. The overlapping portions of the coracoids lie immediately ventral to the heart, which they protect.

Parker designates as 'epicoracoid' the antero-mesial portion which projects slightly from the general contour, while Sabatier applies the same term to the whole cartilaginous portion. Engler, however, shows quite clearly that a true epicoracoid is absent from Urodeles.² It should be noticed in this connexion that the overlapping of the coracoids—known as *arcifery*—is not identical with the Anuran *arcifery* (e.g. Bufo), since in these animals it is the *epi-coracoids* which overlap and not the coracoids.

(d) **The Sternum** (most authors) (Fig. 22).

Cartilaginula quadrata intermedia Funk (1827).

The sternum of the Salamander is a small median cartilaginous plate, lying behind the coracoids. Its shape is roughly that of an equilateral triangle with the apex directed forwards, and a short projection from the middle of the base pointing posteriorly. The sides are grooved to receive the postero-mesial edges of the coracoid cartilages. These grooves are fairly deep and do not merge into one another anteriorly, but are divided by a septum, so that one groove

¹ Cf. Engler (1929).

² Except in *Siren lacertina* and *Cryptobranchus alleghaniensis*.

passes dorsally and the other ventrally across the apex of the triangle. Which side is ventral and which dorsal depends on the relation of the coracoids to one another, since the grooves in the sternum occupy the corresponding relative positions. The sternum is attached to the coracoids by a membrane, *membrana sterno-coracoidea* (Engler), which arises from the *linea alba*, and is also closely attached to the pericardium dorsally, its dorsal surface being slightly concave so as to fit this structure. Although the exact shape is subject to considerable fluctuation, the present writer has never seen a sternum with the long anterior process such as is figured by Perrin, and it would seem that his figure must have been prepared from a very unusual specimen. The sternum serves for the attachment of the pectoralis muscle ventrally, while superficial rectus muscles of the abdomen and neck are attached to its edges, *dorsal* to the coracoids. A very good and detailed account of this structure and of its development is given by Engler.

As may be judged from the above synonyms, the several parts of the pectoral girdle have been homologized with widely different structures. It is perhaps unnecessary to review the somewhat involved discussions here, since the identities of the elements as expressed above are now generally accepted. The most noteworthy papers are those of Gegenbaur (1865), and Parker (1868), while Engler (1929) has recently worked out the ontogenetic history in considerable detail, particularly with regard to the sternum.

2. The Fore-limb (figs. 23-8 and 39-42).

This comprises the usual elements found in a tetrapod fore-limb, namely, the *humerus* in the arm, the *radius* and *ulna* in the fore-arm, *carpals* and *metacarpals* in the wrist, and *phalanges* in the digits.

The chief points of interest are: (i) the peculiar shape of the humerus, and particularly of its proximal end, (ii) the morphology of the carpus and the homology of the digits. Each of these features will be dealt with in the appropriate place. The epiphyses of all the long bones, and all articular surfaces, are cartilaginous.

(a) **The Arm** (Figs. 23, 24, and 42). The long axis of the *humerus* is almost straight. The head is expanded dorso-ventrally in a peculiar manner and merges into the *crista ventralis humeri* (cr.v.h.) The cartilaginous epiphysis at this end when seen in side view is therefore shaped like a comma (fig. 42). The *crista ventralis* is short, occupying only about a third the total length of the bone, but it is of considerable expansion and rises steeply from the shaft. It fits into the notch, already referred to, formed in the rim of the glenoid cavity

by the lips of the coracoid and pro-coracoid, and serves for the attachment of MM. pectoralis and supra-coracoideus. At about the same level on the other side of the bone is the *crista dorsalis humeri* (cr.d.h.). This is a smaller hooked process and does not extend on to the head of the humerus. M. subscapularis is inserted on it. Immediately distal to the point from which these crests arise the humerus is approximately circular in cross-section, but it very soon expands in an axial plane, i.e. at right angles to the expansion of the head. On the pre-axial border of the distal end is the *epicondylus lateralis humeri* (co.l.h.), a fairly pronounced ridge, partly osseous and partly cartilaginous, which gives rise to the MM. extensor antebrachii et carpi radialis, and extensor digitorum communis and, in part, to the M. extensor antebrachii et carpi ulnaris. On the postaxial border is a similar ridge, the *epicondylus medialis humeri* (co.m.h.), from which arise the flexor muscles antagonistic to those above mentioned. The *radial condyle* (co.r.) (*Eminentia capitata*, Gaupp) is large, and forms about two-thirds of a complete sphere, standing out prominently from the surrounding structures towards the ventral, or flexor, surface of the arm. The *ulnar condyle* (co.u.) is much smaller, and is approximately semi-elliptical in shape, while between the two condyles is a shallow *trochlear groove* (fs.tr.). Both condyles and groove are entirely cartilaginous. The *fossa cubitalis ventralis* (fs.cu.v.) (Gaupp), into which the end of the radius fits when the arm is flexed, is very deep and well marked, but the *olecranon fossa* (fs.ol.) is shallow and indefinite.

(b) **The Fore-Arm** (figs. 25-7 and 39-41). The *radius* and *ulna* are completely separate, and of approximately equal length and average size. The proximal end of the *radius*, or pre-axial element (figs. 39-41), is more or less circular in section, and the bone tapers fairly evenly to the middle of the shaft where the smallest diameter is reached; there being only a very small crest on the ventro-mesial surface. The *epiphysial cartilage* of the proximal end is slight and saucer-shaped; its concavity is shallow. The distal end of the radius expands in an axial direction so that, when seen from the extensor or flexor surfaces, it is roughly triangular in shape. The cross-section of this end is approximately rectangular, and the *cartilaginous epiphysis* is more extensive on the pre-axial side than on the post-axial. It articulates with the *pars intermedia* of the fused ulnare + intermedium and also with the *radiale*.

The *ulna* (figs. 25-7), in contrast to the radius, is larger at its proximal end and smaller distally. The club-shaped proximal end is trapezoid in section, the longest side being mesial. The epiphysis

which articulates with the ulnar condyle of the humerus and bears an olecranon process is entirely cartilaginous. The central portion of the shaft is very slender, and is roughly triangular in transverse section, with a slight bony crest running along the flexor side. The distal end is but slightly expanded, and articulates only with the ulnare+intermedium.

To summarize: the radius and ulna are entirely separate. The greatest expansion of the radius is distal, and in an axial direction, while the ulna expands proximally, and in a vertical plane. Both elements articulate with the humerus as well as with the carpus.

(c) **The Carpus** (fig. 28) of the adult Salamander consists of seven elements, namely, the *radiale*, a fused *ulnare+intermedium*, a *centrale*, and four *basalia*. Much has been written concerning the homologies of these basal elements and of the four digits which they bear. The older authors, e.g. Gegenbaur, Wiedersheim, and Hoffmann, supposed that the hand lacked the pre-axial digit, or pollex—apparently by analogy with the normal reduction sequence in the mammalian carpus. When, however, the carpus of the Salamander, or of any other four-fingered Urodele, is compared with the tarsus, which bears five toes, a strong similarity is to be observed in the pre-axial sides of the two limbs. Further, in some forms, e.g. Triton and *Diemyctylus*, there are evident traces of a reduction occurring in the post-axial region of the tarsus (cf. Steiner, 1921). Both Perrin and Sieglbaur have concluded, from a comparative study of the muscles of the hand and foot of *Salamandra*, that the pre-axial digits of each are serially homologous, and that therefore it is the post-axial, or fifth finger, which is missing from the hand, and this is the view adopted here. It should be mentioned that both Ribbing and Eisler, in spite of having investigated the muscles and nerves in detail, apparently retain the older view, although they do not directly discuss the question.

Turning now to the carpalia themselves, the most pre-axial of the basal carpals (c.pr.p.) was considered by Gegenbaur, Wiedersheim, and the earlier authors to be the basal of the second digit (they considered the first digit to be missing entirely) pushed a little out of its place. Strasser (1879), however, by studying the development in Triton and *Salamandra*, showed that primitively this cartilage has no connexion with the pre-axial digit, and that the next basal (his *Basale commune*) has a double origin and is always related, in the larva as well as in the adult, to *each of the first two digits*. He therefore concludes that this element represents *basalia 1 and 2* fused together. In 1886 Kehrler suggested that the preaxial cartilage above referred

to is really the *basal* of a *pre-pollex*, of which digit no further trace has remained. This view was supported by Baur (1888), Rabl (1901), Steiner (1921), and others.

So far as the present investigation of *Salamandra* is concerned the description of the anatomical relations given by these authors has been entirely confirmed, i.e. that the first two digits articulate with a common basal, and that the first basal is not at all closely associated with the first digit, and lies rather more proximally than the other basal elements. Further, in a specimen in which the bones had been stained with alizarin, and the soft tissues cleared with potassium hydroxide and glycerine, it was apparent that the basal common to the first two digits had ossified from two centres, in fact it presented an appearance comparable with that of the fused ulnare+intermedium. Finally, the fact that the short flexor muscles for the first digit take their origin from this element and not from the most pre-axial cartilage seems to add conclusive evidence in favour of Strasser's view. Various other authors have made contributions bearing on the subject, and their views may be summarized, according to whether they support or oppose the conclusions set forth above, as follows.

IN SUPPORT: Strasser (1879); Kehrer (1886); Baur (1888); Emery (1895); Zwick (1898); Rabl (1901); Sewertzoff (1907); Steiner (1921).

OPPOSED: Gegenbaur (1864); Goette (1879); Braus (1906).

It must be pointed out that Sewertzoff and Zwick do not regard the cart. pre-pollicis as having such a status, but rather suppose it to be a supernumerary centrale.

In the carpus of *Salamandra* we have therefore (if the above interpretation be accepted) in the distal row of carpalia, starting from the pre-axial border, a *cartilago pre-pollicis* (c.pr.p.) which remains cartilaginous throughout life; a fused *basale* 1+2 (o.b.c. 1+2) (*Basale commune*, Strasser), with an osseous centre in the adult, serving the first two digits; a *basale* 3 for the third finger, and a *basale* 4 for the fourth, both of which also become ossified in the centre. There is a bony *centrale* (o.c.) which articulates with all the other elements of the carpus with the exception of the *pars ulnaris* (o.u'+i.) of the ulnare+intermedium. The *radiale* (c.rd.) remains entirely cartilaginous. It is relatively small and articulates proximally with the radius, mesially with the *pars intermedia* (o.u.+i'.) of the ulnare+intermedium, and distally with the centrale and cart. pre-pollicis. As already indicated the *ulnare* and *intermedium* fuse in the adult to form a common element, of which the major portion ossifies. The

line of fusion between them is indicated by a foramen, the *for. perforans carpi* (fo.per.c.), through which the A. perforans carpi passes from the ventral to the dorsal side. It is by far the largest element in the carpus, and articulates with the ulna, radius, radiale, centrale, and basale 4.

(d) **The Metacarpals and Phalanges** are all dumb-bell-shaped bones with cartilaginous epiphyses. The digital formula is 1.2.3.2. The homology of the fingers is fully discussed above.

II. THE PELVIC GIRDLE AND HIND-LIMB (Pl. V).

1. The Pelvic Girdle (Figs. 34 and 35).

This girdle is a much firmer structure than the pectoral. It is firmly attached dorsally to the vertebral column, while ventrally the two halves meet one another in a median symphysis. The constituents of the girdle are dorsally a club-shaped member, the *ilium*, and a ventral irregularly shaped plate, the composite *pubo-ischium*. Anterior to this latter portion is a median-forked cartilage, the *cartilago ypsiloidea*, which is only doubtfully to be regarded as a part of the pelvic girdle proper.

The *ilium* (o.il.) (os ischii, Funk) projects dorsally from the acetabulum with a slight backward inclination, and is firmly attached to the rib of the sacral vertebra by fibrous tissue. It is a club-shaped structure with the 'head' directed dorsalwards. The dorsal extremity remains cartilaginous (= the epileon of Sabatier), but the remainder ossifies with the exception of a small area at the junction with the pubo-ischium.

The *pubo-ischium* (ilio-pubis, Funk) is an irregularly shaped plate, approximately quadrangular, forming an inverted arch in the transverse plane. The posterior or ischial part of the plate is always ossified—except at the symphysis—while the anterior or pubic portion is usually pure cartilage, although it may show a varying amount of ossification (cf. Wiedersheim, 1892). In the latter case it is impossible to distinguish the boundary between the pubis and ischium in the adult. The pubis is perforated by a small obturator foramen (fo.o) for N. obturatorius. Anteriorly the lateral part of the pubis is prolonged to a short pre-pubic process (pr.p-p.) while the lateral portion of the ischium projects posteriorly in a similar manner forming an ischial spine.

Both portions of the ventral plate as well as the ilium contribute to the *acetabulum* (ac.) (cavité cotyloïde, Perrin), which is large and roomy, though the rim is not complete at the antero- and postero-

dorsal margins. There are three prominences around its periphery, one dorsal arising from the ilium, one antero-ventral formed from the pubis, and one postero-ventral projecting from the ischium. The head of the femur is firmly attached to the two former points by a pair of *cotyloid ligaments*.

The Cartilago Ypsiloidea (fig. 36) (Townson, 1795).

Cart. marsupial	Dugès (1834).
Abdominal sternum	Sabatier (1880).
Cart. epipubes	.	.	Wiedersheim, Hoffmann (1876), and others.				
Cart. ypsiloides	.	.	Hoffmann (1873-8); Whipple (1906).				

As its name implies this is a Y-shaped cartilage lying in the middle line, anterior to the pubo-ischium with which it articulates. It lies *dorsal* to the M. rectus abdominis and is closely associated with it. As indicated by the synonyms, this cartilage has been homologized with various structures. Whipple (1906) investigated its development, on a limited supply of material, and concludes that it arises in the linea alba as the result of muscle strain, and has nothing to do with the pelvic girdle. Against the view held by Wiedersheim and Hoffmann that this cartilage is homologous with the epipubis of reptiles, she advances the argument that the cart. ypsiloidea develops and remains entirely *dorsal* to the rectus muscle, whereas the marsupial bone is ventral to it.

From observations and experiments on aquatic Salamanders (*Diemyctylus*) Whipple arrived at the conclusion that, in these forms, the ypsiloid apparatus is definitely correlated with the hydrostatic function of the lungs. Thus, by raising the ypsiloid cartilage the animal is able to compress the posterior end of the body cavity and so force the air in the lungs forwards to the anterior end, thus causing the animal's head to rise in the water, while by lowering the cartilage the air is brought back to the posterior end and the head of the animal sinks so that it is able to swim to the bottom. This explanation is of course irrelevant as far as *Salamandra* is concerned, since this animal is purely terrestrial in the adult stage. Nevertheless it is not unreasonable to suppose that it may be of assistance in defaecation and parturition by virtue of its capacity to compress the posterior abdomen.

2. The Hind-Limb (Figs. 29-33).

The form of the hind-limb corresponds with that of the fore-limb except that it bears five digits instead of four. For descriptive purposes it may be divided into three regions: (*a*) the *thigh*, containing

the *femur* as its skeletal element; (*b*) the *leg*, with the *tibia* and *fibula*; and (*c*) the *tarsus* and *digits* supported by the *tarsals*, *meta-tarsals*, and *phalanges*. As in the fore-limb all epiphyses and articular surfaces remain cartilaginous.

(*a*) **The Femur** (Figs. 31-3). The head of the femur is rounded but not hemispherical, since there is a *trochlear groove* on its postero-ventral surface which articulates with the ischial process on the rim of the acetabulum, while the dorsal and antero-ventral surfaces are somewhat flattened and possess well-marked *foveal depressions* (fv.c.fm.) wherein are inserted the ligaments attaching the bone to the acetabulum (l.pb. and l.il.). In transverse section, therefore, the proximal end of the bone is roughly triangular, with the sides facing dorsal, antero-ventral, and postero-ventral. There is no neck, and the articular surface is terminal. There is a strong hook-shaped *trochanter* (pr.tch.) directed antero-mesially on the ventral surface, towards which, from either side of the trochlear groove, run two *trochanteric crests*, of which the posterior is the less developed. The cross-section of the bone beyond the hook is approximately circular but it soon expands into a rectangle of which the long sides are dorsal and ventral. There are two articular condyles distally, the pre-axial or *tibial* being the larger, although neither is so pronounced as the corresponding surfaces of the fore limb. The longitudinal axis of the bone is approximately straight when seen from above, but shows a double curvature if viewed in an axial direction.

(*b*) **The Tibia** (o.tb.) is a straight simple bone whose section is more or less rectangular at the ends and circular at its narrowest part, which is at about one-third of its length from the distal end. The long sides of the proximal end are on the flexor and extensor surfaces, but at the distal end the long axis of the rectangle is at right angles to these. A prominent *tibial crest* (cr.tb. fig. 29) arises from the dorso-mesial side of the extensor surface which finally becomes independent of the surface of the bone so as to give it a thorn-like appearance. It receives the insertion tendon of the M. extensor ilio-tibialis. Distally the tibia articulates with the tibiale and intermedium.

(*c*) **The Fibula** (o.f.) is a rather more slender bone than the tibia but of about the same length. It is roughly triangular in section with the base directed mesially. Its distal end is very oblique and articulates with the fibulare and intermedium.

(*d*) **The Tarsus** (Fig. 29 and 30). The *fibulare* (o.fb.) is the largest of the proximal row of tarsal elements, and is *not* fused with the

intermedium like the ulnare in the carpus. The *intermedium* (o.i.) is a wedge-shaped bone of which the thinner edge projects between the tibia and fibula, thus separating the distal ends of these two bones. Distally it articulates with the centrale, fibulare, and tibiale. Its post-axial border is slightly notched to allow the A. perforans tarsi to pass from the ventral to the dorsal side of the ankle. The *tibiale* (c.t.) is the smallest element of the proximal row. It is helmet-shaped and articulates with the tibia, intermedium, centrale, and the cartilago pre-hallucis. Normally it remains cartilaginous. The *centrale* (o.c.) is very large and articulates with all the other elements of the tarsus except the basal tarsal of the fifth digit. The *basalia* of the tarsus are strictly comparable with those of the carpus. The pre-axial represents the basal of a *pre-hallux* (c.pr.h.), the next is a *basale commune* (o.b.t. 1 + 2) bearing the first two digits, while the remaining three are smaller, each supporting one digit only. All become more or less ossified except the basal of the pre-hallux. The *meta-tarsals* and *phalanges* are all dumb-bell-shaped bones and the digital formula is 1.2.3.2.

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IV

THE MUSCLES

GENERAL LITERATURE.

MOST of our modern knowledge of the muscles of the Salamander is due to the work of specialists who, taking some small part of the body, have endeavoured to work out the comparative morphology of the muscles concerned throughout the vertebrate series. Nevertheless a few of the earlier workers have described the chief muscles in a general sort of way, naming them according to their position, or to their apparent resemblance to a muscle in the human body. Thus Funk (1827) gives quite a passable account of all the principal muscles, and a year later Carus (1828) also described and figured them very well indeed. Dugès (1834) names and figures a large number, but his text is so scanty that it is frequently impossible to be sure of the identity of the muscle concerned. In 1852 Rymer Jones, in his article on 'Reptilia' in Todd's *Cyclopaedia of Anatomy and Physiology*, gives two figures of the muscles of Salamandra (taken from Carus without acknowledgement) and describes the principal muscles. Some idea of the extent of the work of these authors may be obtained from the lists of synonyms preceding the account of each muscle described below. The endeavour has been made to get these lists as complete as possible, and in addition to the names actually applied to the muscles of Salamandra itself those given to the homologous muscles of Cryptobranchus by Humphry, Schmidt, Goddard and van de Hoeven, and by Osawa, have also been appended for comparative purposes. The figures reproduced in Owen's text-book, although credited to Funk by Owen, do not occur in Funk's monograph but are due to Carus (1828).

A review of the more specialized literature precedes the anatomical description in each of the subsequent sections.

MUSCLES OF THE HEAD

1. Historical.

Rusconi (1854) gives a very good account of the visceral muscles and of the changes which they undergo during metamorphosis. His work is general rather than detailed, as would be expected from its date. In 1887 Walter also gives a good account of the visceral

skeleton and its related muscles in Urodeles, Anura, and Reptiles, but it was Wilder (1892 and 1896) who first gave an exact description of the larynx and its muscles. He endeavoured to homologize the latter with those of the visceral arches. A brief résumé of his hypothesis and of those of subsequent workers in this field is given on p. 272. Further contributions to the discussion of the homologies of the laryngeal muscles were made by Göppert in 1894 and 1898. In 1902 Burkard undertook a comparative study of the muscles surrounding the orbit in the various classes of vertebrates, and included a description of the *M. levator bulbi* of *Salamandra*. A very detailed and exact description of the muscles supplied by the VIIth, IXth, Xth, and hypoglossal nerves in *Salamandra* and *Triton* was published by Drüner in 1901. He also describes the nerves themselves and the hyobranchial skeleton. Two years later (1903), and again in 1904, Drüner supplemented this account by describing the same region in other Urodeles, and included some theoretical considerations on the homology of the chorda tympani, and of the larynx. His whole work is a classic and very accurate. A comparative study of the jaw-muscles of vertebrates was published by Lubosch in 1913 and 1914, and while he does not deal with *Salamandra* itself, his work is important from a comparative point of view. In 1914 Luther described the muscles supplied by the Vth nerve, which include the *M. levator mandibulae* and the *M. levator bulbi*. He deals with *Salamandra*. Lastly Edgeworth (1920 et seq.) has published many papers dealing with the development and homologies of the muscles of the head in Amphibia and other vertebrates, and was the first to show that the larynx and its muscles have no phylogenetic relationship with the visceral arches. It is Edgeworth's nomenclature which has been adopted here.

2. Muscles of the Eye (Pl. XIII, fig. 57).

These are eight in number, namely, four recti, two oblique, together with the MM. levator and retractor bulbi. Of these, seven are described below, while the eighth—the *M. levator bulbi*—belongs to the muscles of the Vth nerve and is described on p. 55.

M. rectus superior (m.r.s.).

This muscle arises from the dorso-posterior angle of the orbit and runs antero-laterally, broadening somewhat at its insertion on the dorsal section of the ambitus of the bulbus oculi. Its origin is tendinous.

Innervation: By the superior ramus of N. oculomotorius (third cranial nerve).

Function: See below.

M. rectus posterior (m.r.p.).

The abducent muscle arises as a fine tendon from the orbito-sphenoid at about a third of its length from the posterior end, just behind the M. rectus inferior. It passes obliquely postero-laterally, ventral to the M. retractor bulbi, and is inserted in the postero-lateral portion of the eyeball. Like all the rectus muscles it broadens considerably towards its insertion.

Innervation: From the abducent nerve (sixth cranial).

Function: See below.

M. rectus inferior (m.r.i.).

The inferior rectus muscle also has a tendinous origin just anterior to that of the posterior rectus and posterior to the anterior rectus. It is considerably shorter than the muscle just described, and somewhat broader. It runs laterally, its fibres lying almost at right angles to the axis of the skull. Its insertion occupies the ventral section of the ambitus of the bulbus.

Innervation: From the inferior ramus of the N. oculomotorius (third cranial nerve).

Function: See below.

M. rectus anterior (m.r.a.).

As mentioned above, the tendon of this muscle leaves the orbito-sphenoid just anterior to that of the inferior rectus. Its fibres take a direction practically at right angles to those of the former muscle and lie close along the side of the skull. They are inserted on the antero-mesial surface of the bulbus oculi. It is the largest and strongest of the rectus muscles.

Innervation: From R. inferior N. oculomotorius.

Function: The function of all the rectus muscles is obviously to rotate the eyeball in the horizontal and vertical planes at right angles to its own optical axis. They are all relatively weak.

M. obliquus superior (m.o.s.).

Arises as a fine tendon from about the centre of the *cartilago antorbitalis* of the nasal capsule. Its fibres run posteriorly and are inclined slightly mesialwards. They are inserted on the antero-dorsal portion of the eyeball just anterior to those of the M. rectus superior. The muscle lies dorsal to the main portion of the

N. ophthalmicus profundus (V_1) although an important cutaneous branch of this nerve crosses its dorsal side (see p. 139).

Innervation: By N. trochlearis (fourth cranial nerve).

Function: See below.

M. obliquus inferior (m.o.i.).

Like its superior counterpart this muscle arises from about the middle of the *cart. antorbitalis*. It passes in a postero-ventral direction and is inserted on the ventral side of the eyeball. It has rather a long insertion on a line approximately at right angles to the optical axis, so that the lateral fibres are much shorter than the mesial ones.

Innervation: From the R. inferior N. oculomotorius.

Function: The oblique muscles serve to rotate the eyeball about the optical axis. Both are, however, very weak.

M. retractor bulbi (or *oculi*) (m.rt.b.).

This is by far the most powerful of all the eye-muscles. It takes its origin in part from the lateral process of the parasphenoid that lies under the otic capsule, and in part from the orbito-sphenoid at the inner ventral angle of the orbit. Its fibres spread out to form a cone around the optic peduncle and are inserted on the mesial surface of the bulbus oculi within the ring formed by the rectus muscles. The cone is, however, not complete, since the edges of the muscle are not quite in contact mesially in the region of the anterior rectus muscle.

Attached to the M. retractor bulbi is a strong tendon connecting it with the eyelids. This tendon forms a broad sheet posteriorly but bifurcates anteriorly to allow for the passage of the anterior rectus muscle. When this tendon is pulled the edges of the eyelids are brought together and the eye closed, and although there appear to be smooth muscle elements in the upper lid rendering it capable of independent movement, nevertheless the M. retractor bulbi and the tendon must be regarded as the chief agents effecting the closing of the eye, which is thus made to occur simultaneously with the retraction of the bulbus oculi.

Innervation: From the N. abducens (sixth cranial nerve).

Function: To retract the bulbus and to close the eyelids as described above.

3. Muscles of the Fifth Nerve.

M. levator mandibulae as a whole.

Élévateurs de la mâchoire inférieure	.	.	.	Meckel (1818).
Temporalis	.	.	.	Cuvier (1835); Owen (1866).
Adductor mandibulae	.	.	.	Drüner (1901).
Masseter	.	.	.	Wilder (1891).

This muscle is divided by all modern authors into three main sections which are named according to their position relative to the mandibular branch of the Vth nerve.

M. levator mandibulae anterior (Edgeworth).

Temporalis	v. Siebold (1828); Cuvier (1835); Fischer (1843); Schmidt, Goddard, and van d. Hoeven (1864); Mivart (1869); Drüner (1901); Coghill (1901-6); Osawa (1902)
Post-orbito-coronoïdien et Atlanto-coronoïdien	Dugès (1834).
Ptérygoïdien	Rusconi (1854).
Atlanto-mandibularis	Owen (1866).
Pterygo-temporalis	v. Plessen & Rabinowicz (1891).
Cranio-mandibularis (partim)	Lubosch (1914).
Adductor mandibulae internus	Luther (1914).

This muscle lies wholly mesial to the mandibular branch of the trigeminal nerve (V_3). It is divisible into two distinct portions, and most modern authors have thus distinguished a superficial and a deep layer.

M. levator mandibulae anterior (superficial portion) (Edgeworth).

Temporalis (3rd portion)	Funk (1827); Cuvier (1835); Fischer (1843); Lubosch (1914).
Crotaphite	Rusconi (1854).
Pseudo-temporalis	Luther (1914).

This is a long, narrow, conical muscle which arises partly from the lateral border of the *parietal*, and partly from the dorsal fascia that extends from the skull to the neural spine of the first vertebra, but mainly from a strong raphe which passes from the neural spine of the first vertebra through the centre of the muscle, the fibres arising from either side of it, forming a pinnate structure. The muscle crosses dorsally over the skull in the otic region, and then turns downwards in front of the ear capsule almost at right angles, and passes into a strong tendon which is inserted in the coronoid process of the pre-articular element of the lower jaw.

M. levator mandibulae anterior (deep portion) (Edgeworth).

Frontales	Funk (1827).
Pterygoideus	Cuvier (1835); Fischer (1843); Owen (1866); Drüner (1901); Lubosch (1914); Luther (1914).
Ptérygoïdien	Rusconi (1854).
Pterygo-maxillaris	Hoffmann (1873-8).

A short, fan-shaped, almost vertical muscle. Its fibres arise from the lateral borders of the *frontal* and *parietal* elements of the skull and

converge to a long band-like tendon which is attached to the dorsal margin of the pre-articular, immediately anterior to the articulation of the jaw. It is largely covered by the superficial portion, the fibres of which tend to mingle with it near its insertion.

Innervation: Both portions of the muscle are innervated by a special branch of the trigeminus nerve which leaves it either just before, or just after it emerges from the antrum petrosum laterale.

Function: Both portions assist in closing the mouth.

M. levator mandibulae posterior (Edgeworth).

Cranio-mandibularis (partim)	.	.	.	Lubosch (1914).
Adductor mandibulae posterior	.	.	.	Luther (1914).

A somewhat triangular-shaped muscle arising from the free anterior edge of the *squamosal*, the anterior face of the *quadrate*, and the *pterygoid*. It is traversed by the mandibular nerve (V_3) so that, while some of its fibres lie mesial, the greater portion of the muscle lies posterior to that nerve. A portion of the muscle has a fleshy insertion on the articular portion of Meckel's cartilage, while a tendon passes forwards from the anterior fibres to a point immediately in front of the tendon of the *M. levator mandibulae anterior* (superficial portion), some of the mesial fibres being actually inserted on the tendon of this muscle. The general direction of the fibres is, therefore, antero-ventral, the most anterior fibres being of moderate length and the most posterior extremely short.

Innervation: By fine twigs from the mandibular nerve.

Function: To assist in closing the jaws.

M. levator mandibulae externus (Edgeworth).

Masseter	Funk (1827); v. Siebold (1828); Fischer (1843); Rusconi (1854); Schmidt, Goddard and van d. Hoeven (1864); Owen (1866); Mivart (1869); v. Plessen & Rabinowicz (1891); Drüner (1901); Coghill (1901-6); Osawa (1902).
Temporal, portion postérieure courte	Cuvier (1835).
Pré-temporo-maxillaire	Dugès (1834).
Petro-tympano-maxillaris	Hoffmann (1873-8).
Mandibularis externus	Lubosch (1914).
Adductor mandibulae externus	Luther (1914).

This muscle lies anterior to the one just described and entirely lateral to the mandibular nerve, the direction of its fibres being parallel with those of the *M. lev. mand. post.* It takes its origin from the antero-lateral edge of the *squamosal* and from the anterior wall of the ear capsule, and is inserted on the posterior end of the *dentary* and the lateral face of the coronoid process of the

pre-articular. The skin at the corner of the mouth is strongly reflexed dorsalwards and is firmly bound to the anterior portion of this muscle—in fact some of the fibres seem actually to be inserted on it. Like that of the previous muscle the insertion is fleshy posteriorly with a tendency to become tendinous anteriorly.

Innervation: By fine twigs from the mandibular nerve (V_3).

Function: To assist in closing the mouth. The *M. levator mandibulae* in general is opposed by the *M. depressor mandibulae*, a muscle supplied by the VIIth nerve.

M. intermandibularis (Edgeworth) (Pl. VI, fig. 37).

Mylohyoideus	v. Siebold (1828); Carus (1828); Stannius (1854);
	Owen (1866); Coghill (1901-6).
„ (et interhyoideus)	Walter (1887).
„ (et interhyoideus et interhyoideus posterior)	Funk (1827).

As its name implies this is a sheet of muscular tissue stretching across the floor of the mouth between the rami of the lower jaw. It lies immediately under the skin. In the larva it consists of two distinct parts, a small anterior portion lying in the angle of the chin, and a larger posterior portion. It is the latter only which is found in the adult after metamorphosis, but the synonyms of the anterior portion are given below for the sake of completeness.

M. intermandibularis anterior. Drüner (1901); Luther (1914); Edgeworth (1920 et seq.).

Submentalis	Fischer (1843); Mivart (1869); Osawa (1902).
Genio-glossus	Schmidt, Goddard and van d. Hoeven (1864).
Submaxillaris	Hoffmann (1873-8).
C_2 mv (antr.)	Ruge (1897).

A purely larval muscle, aborting at metamorphosis.

M. intermandibularis posterior (m.i.m.). Drüner (1901); Luther (1914); Edgeworth (1920 et seq.).

Mylohyoideus anterior	Fischer (1843); Mivart (1869); Osawa (1902).
Partie antérieure du mylohyoïdien	Rusconi (1854)
Mylohyoideus	Schmidt, Goddard and van d. Hoeven (1864).
Intermaxillaris anterior	Hoffman (1873-8); v. Plessen and Rabinowicz (1891).

C_2 mv (post)	Ruge (1897).
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From the above list of synonyms it will be seen that certain authors have called this the *anterior* part of the muscle, owing to the fact that they have mistaken the *M. interhyoideus* for the posterior part.

The *M. interhyoideus* is a VIIth nerve muscle, however, and its connexion with the mandible is secondary.

The *M. intermandibularis posterior* arises from the anterior two-thirds of the mesial upper edge of each ramus of the mandible except for a very short distance near the middle line anteriorly, which latter gives rise to the *M. genio-glossus*. The fibres run transversely across the space between the two rami of the lower jaw, but are interrupted in the middle line by a wide aponeurosis of tough transparent connective tissue, the *linea alba*. In a fresh specimen the *MM. genio-hyoideus* and *genio-glossus* are seen through this aponeurosis and the *M. intermandibularis* looks as though it were inserted into their edges.

Innervation: From *N. mandibularis* (*R. intermandibularis*).

Function: The contraction of this muscle serves to elevate the mouth floor, and it is therefore of service in breathing and deglutition.

M. levator bulbi (Pl. IX, fig. 53). Hoffmann (1873-8); Drüner (1901); Burkard (1902); Luther (1914); Edgeworth (1920 et seq.).

Fronto-ptérygoidien Dugès (1834).

An excellent description of this muscle has been given by Luther (1914) and his nomenclature has been adopted here. His anatomical results, as far as the adult is concerned, are accurate, but his conclusions regarding the phylogenetic history of the muscle do not agree with those of Edgeworth.

It is by no means easy to determine the direction of the fibres in the several portions of this muscle, but the application of a little dilute saffranin is of material assistance.

The muscle consists of a thin sheet forming an elastic floor to the orbit and lies between the *bulbus oculi* and the roof of the mouth, ventral to the *MM. rectus* and *obliquus inferior*. Luther distinguishes the following three sections.

(a) The *pars principalis* (m.l.b.p.) is the most dorsal portion, lying nearest to the *bulbus oculi*. It arises as a thin, tough, tendinous sheet from the lateral borders of the *parietal*, *frontal*, and *pre-frontal* elements of the skull as far as the *cartilago antorbitalis* of the nasal capsule. The fibres run mainly in a postero-lateral direction and converge so as to form a more or less scimitar-shaped plate. They are inserted on the ventral side of the posterior end of the lower eyelid (*membrana nictitans*).

(b) The *pars sagittalis* arises from the palato-quadrate at the posterior wall of the orbit, and may be further subdivided into two heads.

(i) The fibres of the *caput laterale* (m.l.b.s'.) pass obliquely antero-laterally and are inserted along the lower eyelid from a point immediately anterior to the insertion of the *pars principalis* to about the centre of the eyelid.

(ii) The fibres of the *caput mediale* (m.l.b.s'').) pass antero-mesially and are attached to the side wall of the skull immediately ventral to the origin of the *pars principalis*. This portion loops across the origin of the *M. retractor bulbi*.

(c) The *pars transversalis* (m.l.b.t.) takes its origin from the side wall of the skull—mainly from the lower edges of the *frontal* and *parietal*—anterior to the insertion of the *caput mediale*, *pars sagittalis*, and ventral to the origin of the *pars principalis*. Its fibres are the most ventral of all, and pass across the anterior portion of the floor of the orbit forming an arch which is convex anteriorly. They are inserted on the lower eyelid anterior to the *caput laterale*, *pars sagittalis*, and on the maxilla.

Innervation: All sections are innervated by the second branch of the trigeminus nerve (V_2) in the Salamander.

Function: The muscle as a whole appears to have at least two principal functions: (i) as levator bulbi, (ii) as accessory respiratory muscle by enlarging the mouth cavity. It may also serve as an adductor of the lower lid, but the movement thereby caused must be very slight, even if it exists at all (cf. Johnson, 1926).

4. Muscles of the Seventh Nerve.

As already mentioned, an accurate description of these muscles in both larva and adult, illustrated by excellent figures, was published by Drüner in 1901. He divides the muscles supplied by the VIIth nerve into two groups, according to whether they are supplied by the nerve *before*, or *after*, it has received the R. communicans IX+X ad VII, on the supposition that this ramus contains motor fibres. By comparison with the condition in other Urodeles this conjecture appears unwarranted, and it seems more likely that the R. communicans contains only general cutaneous and communis fibres, and therefore has no influence on the muscular supply. Drüner's classification is accordingly unnecessary.

M. depressor mandibulae (Edgeworth).

Depressor maxillae inferioris	v. Siebold (1828).
Témporo-angulaire	Dugès (1834).
Digastricus	Fischer (1843); Stannius (1854-6); Osawa (1902).
Digastrique	Cuvier (1835); Rusconi (1854).

Occipito-mandibularis s. Digastricus	Owen (1866).
Digastric	Mivart (1869).
Digastric et Depressor mandibulae	Humphry (1872).
Cephalo-dorso-maxillaris s. Digastricus-maxillae	Hoffmann (1873-8).
C ₂ md	Ruge (1897).
Cephalo-dorso-mandibularis	Drüner (1901).

A thick, powerful muscle originating from the posterior edge of the squamosal, the 'crista muscularis' of the ear capsule, and the anterior portion of the *fascia cephalodorsalis* (Drüner). This superficial dorsal fascia gives origin to a number of muscles. It is firmly united to the skin and extends backwards to behind the shoulder. Edgeworth (1931) has shown that the M. depressor mandibulae is derived from the M. levator hyoidei of the Dipnoi.

Innervation: From R. jugularis VII by a fine branch which separates from the main nerve immediately distal to the point at which the R. communicans IX+X ad VII is received. It enters the muscle mesially.

Function: As its name implies, it is the opening muscle of the lower jaw and opposes the levator mandibulae.

The *M. interhyoideus* (Pl. VI, fig. 37) is the next muscle to be considered. It undergoes a rather considerable change during metamorphosis, and becomes divided into two portions. The anterior portion retains more or less the original position and therefore retains also the original name—M. interhyoideus, while the posterior portion shifts backwards and hence becomes the M. interhyoideus posterior. Most of the earlier authors regarded the whole muscle as the posterior part of the 'Mylohyoideus'. Both portions together are spoken of as 'Duo-cutis musculi oriuntur in maxillae inferioris unco' by Carus (1828).

M. interhyoideus (Edgeworth) (m.i.hy.).

Constrictor pharyngis internus	v. Siebold (1828).
Mylohyoidien, portion moyenne	Rusconi (1854).
C ₂ hv	Ruge (1897).
Inter-ossa-quadrata	Drüner (1901).

The origin of this muscle is by means of a short thin tendon from the postero-mesial edge of the quadrate, just ventral to the point of insertion of the *ligamentum hyoquadratum*. According to Drüner some fibres may occasionally arise from the ligament itself. The fibres spread out fan-wise over the hinder part of the mouth-floor, and are inserted into a posterior continuation of the median aponeurosis of the M. intermandibularis posterior. The direction of the most posterior fibres is thus almost directly transverse and that of

the anterior ones obliquely antero-mesial. The mesial ends of the anterior fibres lie dorsal to the M. intermandibularis posterior.

While this portion of the muscle retains its original position, its origin has nevertheless shifted, and has migrated from the posterior end of the hyoid arch, passing up the lig. hyoquadratum to the quadrate.

Innervation: By the terminal branches of R. jugularis VII which spread over its ventral side.

Function: It constricts the hyobranchial skeleton and posterior part of the mouth, and thus assists both in respiration and deglutition.

M. interhyoideus posterior (Edgeworth) (m.i.hy.p.).

Constrictor pharyngis externus	v. Siebold (1828).
Mylo-hyoidien, partie postérieure	Rusconi (1854)
Mylosternoideus	Walter (1887).
C ₂ vd	Ruge (1897).
Quadrato-pectoralis	Drüner (1901).

The posterior portion of the interhyoid muscle arises by means of a strong tendon from the ventro-lateral surface of the *quadrate* and the distal end of the *squamosal*. Its fibres spread out fan-wise across the throat ventral to those of the preceding muscle. The muscle becomes joined to the capsule surrounding the articulation of the jaw as it passes laterally across it. The direction of the anterior fibres is almost transverse, and they are inserted in backward continuation of the same aponeurosis as receives the MM. intermandibularis and interhyoideus. The most posterior fibres, forming the bulk of the muscle, turn more postero-mesially and are inserted into the skin at the gular fold. This fold of skin surrounds the throat on the ventral side, and represents the remains of the gill operculum of the larva fused with the skin of the pectoral region. To the same fold, posteriorly, is attached the base of a triangular aponeurosis—the *fascia pectoralis* (Drüner)—the apex of which is directed backwards and is attached to the most anterior fibres of the M. pectoralis, so that by this means the two muscles, the M. interhyoideus posterior and the M. pectoralis are to some extent associated. The M. interhyoideus posterior lies ventral to the MM. procoraco-humeralis and supracoracoideus, which arise from the pectoral girdle, and is loosely attached to them by connective tissue.

This muscle is peculiarly an adult structure, and Drüner was somewhat doubtful as to its derivation, but thought that it might have arisen from the M. interbranchialis 1. Edgeworth, however,

holds that it is derived from the posterior fibres of the M. interhyoideus which have shifted their origin in a similar manner to the main portion, and have also migrated backwards and obtained a secondary attachment to the skin of the gular fold.

Innervation: From R. jugularis VII, which bends over the posterior edge of the muscle at its origin and then enters it from the dorsal surface.

Function: The muscle must obviously act in more than one way. In so far as it acts as a constrictor of the pharynx—the anterior fibres in particular—it must be of importance in swallowing food and in breathing, while, by virtue of their attachment to the skin and to the *fascia pectoralis*, the simultaneous contraction of the posterior fibres on both sides would tend to depress the head, and the contraction of one side at a time would cause the head to incline sideways.

The three muscles just described are all superficial, and are seen directly the skin is removed. In order to expose the remainder of the hyobranchial muscles it is necessary to cut along the linea alba, and turn back the MM. intermandibularis and interhyoidei.

M. subhyoideus (Drüner, in *Ellipsoglossa*) (m.s.hy.).

Cerato-glossi externi	Funk (1827).
Os hyoides protrahens (14)	Carus (1828).
Geniohyoideus anticus et posticus	v. Siebold (1828).
Genio-hyoideus lateralis	Drüner (in Sal. 1901).

This is the last of the VIIth nerve muscles. It arises from the posterior end of the *cerato-hyal*, which it encloses in a sort of muscular cup. It is narrow and ribbon-like in form, and its fibres run approximately parallel with and ventral to the cartilage from which it arises. The muscle widens a little at its insertion, which is on the dorsal side of the aponeurosis of the M. intermandibularis.

The homology of this muscle is in some doubt. Drüner regarded it as the anterior portion of the larval interhyoideus, and its position and innervation are certainly in agreement with this view. On the other hand, the work of Miss Louise Smith (1920) on the development of the hyobranchial muscles of *Spelerpes* seem to be against it. Miss Smith describes muscle which she calls 'genio-hyoideus lateralis' which appears to be homologous with the muscle just described. Nevertheless, in *Spelerpes*—according to Miss Smith—it is proliferated *not* from the anlage of the interhyoideus but from that of the genio-hyoideus. Now the M. genio-hyoideus is a muscle belonging to the hypoglossal (first spinal) nerve, and all muscles derived from the same anlage should be innervated

by the same nerve, whereas in *Salamandra* the *M. subhyoideus* is innervated by the seventh cranial nerve. To add to the confusion, Elizabeth Szamoylenko (1904) in describing the hyobranchial muscles of the adult *Spelerpes* states that the *M. genio-hyoideus lateralis* is innervated by the N. glossopharyngeus in *both Spelerpes and Salamandra*—which is wrong for the latter animal at least—with the addition in the former of fibres from NN. spinales 1, 2, and 3.

In the face of this conflicting evidence it is not possible to give a decisive verdict without a complete re-investigation of the development of the muscles concerned in both *Salamandra* and *Spelerpes*—an undertaking beyond the scope of the present work. In the meantime a non-committal name (which has been used by Drüner for what appears to be the homologous muscle in *Ellipsoglossa*) has been adopted, and it may be suggested that, in *Salamandra*, the muscle is most probably a true interhyoideus, and is *not* homologous with the muscle occupying a similar topographical position in *Spelerpes*.

Innervation: From R. jugularis VII by means of very fine fibres which enter the muscle on its ventral aspect after penetrating the *M. interhyoideus*.

Function: The contraction of the muscle pulls the dorsal end of the cerato-hyal antero-ventrally, thus causing the cartilage to tip, and so force the anterior end thereof, with its overlying tongue, to move antero-dorsally. It is thus the elevator of the tongue.

5. Muscles supplied by the Ninth and Tenth Nerves.

M. subarcualis rectus 1 (Edgeworth) (m.s.r. 1).

Cerato-glossi-interni	Funk (1827).
Alter (<i>M. os hyoides protrahens</i>) (15)	Carus (1828).
Ceratoglossus	v. Siebold (1828).
Pré-stylo-prébranchial	Dugès (1834).
Cerato-hyoideus internus	Fischer (1843); Mivart (1869); Hoffmann (1873-8); Walter (1887); Drüner (1901).	
Protracteur de la corne hyoïdienne postérieure	Rusconi (1854).
Cerato-hyoideus	Stannius (1854-6).
Cerato-hyoideus externus	Osawa (1902).

This muscle is very similar in appearance to the *M. subhyoideus*, since it bears the same relation to the cerato-branchial 1 as does that muscle to the cerato-hyal. It arises from the dorsal side of the posterior end of the first cerato-branchial cartilage by means of a pinnate raphe, from which the fibres radiate around the end of the cartilage so as to enclose it in a muscular cup. This cup is more

complete, and larger, than that formed at the origin of the M. subhyoideus. The fibres run more or less parallel with the cartilage on its ventral side, and are inserted on the ventro-anterior border of the expanded anterior end of the cerato-hyal. It thus forms a muscular link connecting the opposite ends of the two cartilages.

Innervation: By several fine twigs from the N. glossopharyngeus (IXth) which passes along its dorso-mesial border, and also from a nerve formed by the fusion of twigs from the recurrent branches of the nerves of the visceral arches (Xth).

Function: The obvious result of the contraction of this muscle is to advance the branchial arches, and their associated copula, relative to the cerato-hyal, and, since the movement of this latter element in a posterior direction is limited by the lig. hyoquadratum, the muscle is able to have a positive effect on the branchial apparatus relative to the jaws as well. It also serves to transmit to the branchial arches the movement occasioned by the M. subhyoideus.

Drüner (1901, p. 526) gives an admirable account of the action of these two muscles in extruding the tongue to secure food, based on experiments carried out by him on pithed animals, consisting of applying an electrical stimulus to the nerves concerned, and also on observations made on the living animal. The substance of his account is given below.

As already explained, the action of the M. subhyoideus is to advance the cerato-hyal, first in an antero-dorsal direction, and later to tip the anterior end of the cartilage more dorsalwards. Now if the jaw is simultaneously opened wide, as it is in snapping at prey, the effect is to cause the dorsal surface of the tongue to face directly forwards, the action of the M. subhyoideus alone being about sufficient to bring the surface of the tongue to the level of the snout. The cerato-hyal being held in this position by the M. subhyoideus, its anterior end becomes a *punctum fixum* for the M. subarcualis rectus 1, which, by its rapid contraction, forces the branchial arches and the copula, together with the tongue, still farther forwards. The muscle also pulls the posterior end of the cerato-branchial 1 ventralwards, causing the arches to twist about the copula and thus to force it still farther forwards. The combined result of these operations is to project the tongue to a surprising distance in front of the mouth so as to secure the prey on its sticky dorsal surface. The tongue, with its adhering food, is returned to the mouth by the action of muscles subsequently to be described—MM. hyoglossus and rectus cervicis. When the mouth has been shut the MM. subhyoideus and subarcualis rectus 1 again come into play so as to force the tongue

against the pre-vomerine teeth, and thus assist in working the food backwards to the pharynx so that it can be swallowed.

The whole operation is performed with lightning-like rapidity, but the action is easily observed in the living animal by putting it in a glass receptacle, and allowing a small worm or slug to crawl down the side. In snapping at it the Salamander not infrequently gets its jaws momentarily wedged open against the glass with the tongue protruded, so that its action may be seen.

It will have been noticed that the Salamander uses a very different method in securing its food from that of the Frog. In the latter animal the tongue is freely mobile, and it is this organ alone which is extruded, the skeleton of the hyoid taking but little part in the operation. In the Salamander, on the other hand, the tongue is securely fixed to the floor of the mouth, so that its movement carries with it the whole mouth floor and the hyobranchial skeleton as well.

M. cephalo-dorso-subpharyngeus (mihi)¹ (m.c.ph.).

Dorso-trachealis	Fischer (1843); Osawa (1902).
Constrictor pharyngis	Mivart (1869).
Cephalo-dorso-pharyngeus	Drüner (1901).

This is a compound muscle formed from the *M. transversalis ventralis* iv and the *MM. levatores arcuum branchiarum* iii and iv of the larva (Pl. XXIII, fig. 77).

It arises dorsally by two heads, the anterior arising—together with the anterior part of the *M. cucullaris*—from the *crista muscularis*, a ridge formed by the squamosal above the ear capsule. The posterior head arises from the *fascia dorsalis* together with the posterior portion of the *M. cucullaris* and the *M. depressor mandibulae*, and lies deep to the latter muscle, between it and the *M. cucullaris*. The direction of the anterior fibres is obliquely postero-ventral, while the posterior ones pass ventralwards practically at right angles to their origin, so that the whole muscle forms roughly a right-angled triangle of which the origin is the base and the anterior edge the hypotenuse. The ultimate insertion of the whole muscle is a very strong fibrous tendon, firmly attached in the middle line dorsally to the pharynx, just in front of the larynx, and ventrally to the truncus arteriosus. A short distance on either side of this median tendon is another tendinous inscription dividing the muscle into two portions, namely, a *pars subpharyngea* (*pars ventralis*, Drüner) and a *pars dorsalis* (Drüner), the former lying mesial and the latter lateral to the inscription. A comparison with the larva shows that the *pars subpharyngea* is the

¹ This name has been adopted in consultation with Dr. F. H. Edgeworth.

transformed larval *M. transversus ventralis* iv, while the *pars dorsalis* represents the larval *MM. levatores arcuum branchiarum* iii and iv, and the inscription itself takes the place of the atrophied ceratobranchial cartilages iii and iv. The relation of the two parts of the *pars dorsalis* is also interesting. They are almost always separated by the 'third' aortic arch, or its vestigial remains, so that the portion of the muscle representing the *M. lev. arc. branch. iii* of the larva passes between the systemic arch and the 'third', while that representing the *M. lev. arc. branch. iv* passes between the 'third' arch and the pulmonary. The only exception so far recorded is one case reported by Drüner in which the whole muscle passed posterior to the 'third' arch, between it and the pulmonary.

Innervation: *Pars subpharyngea* from the *R. recurrens n. intestinalis* X, *Pars dorsalis, anterior portion* from the nerve of the fifth visceral (third branchial) arch, and the *posterior portion* from the *R. intestino-accessorius* X. These nerves are exceedingly fine and enter the muscle from its mesial aspect. They are best seen from a dorso-lateral view, by separating the muscle from its origin and carefully turning it out laterally, when the nerves may be seen running across the space against the darker blood-vessels beneath.

Function: One obvious function of the muscle is to constrict the pharynx, and thus it is probably of use in deglutition and respiration; but, as Drüner rightly points out, the intimate connexion between the insertion of the muscle and the truncus arteriosus may cause it to have some effect on that organ. Again, the distal part of the 'third' arch and the ductus Botalli between the pulmonary and systemic arches both pass mesial to the *pars dorsalis*, so that the contraction of the muscle would tend to compress these vessels against the wall of the throat and may thus have some influence in separating the arterial from the pulmonary blood. It is not possible to estimate its exact function, if any, in this respect without physiological experiments on the living animal.

M. dilatator laryngis (Edgeworth) (m.d.l.).

Dilatator aditus laryngis Henle (1839).

Dorso-laryngeus et Dorso-trachealis Fischer (1843).

Dorso-laryngeus et Dorso-trachealis, s. Dorso-branchialis v.

Wilder (1892-6).

Dorso-pharyngeus of Dorso-laryngeus et Dorso-trachealis

Göppert (1894-8).

Dorso-laryngeus Drüner (1901); Osawa (1902).

This muscle is narrow and ribbon-like and arises from the dorsal

fascia lateral to the M. cucullaris and immediately posterior to the muscle just described. It passes ventralwards round the pharynx mesial to the thymus gland, and posterior to the pulmonary arch. It is inserted by means of a strong thread-like tendon—the *ligamentum dorso-laryngeum* (Drüner)—on the *processus muscularis* at the side of the cartilago lateralis of the laryngeal skeleton. The muscle narrows considerably at its insertion and becomes somewhat spindle-shaped.

The muscle has every appearance of being a serial homologue of the M. cephalo-dorso-subpharyngeus, that is to say, it *looks* as though it were descended from a levator arcuum branchiarum posterior to the M. lev. arc. branch. iv, and indeed several notable authors have attempted to prove it to be such a muscle. Edgeworth (1920), however, has shown definitely that this is not the case, and that the resemblance is apparent rather than real. A more detailed discussion of the various theories concerning the homology of the larynx is given on p. 272.

Innervation: From the N. intestino-accessorius X by fine twigs which enter the mesial aspect of the muscle, and also by a branch from the R. recurrens intestinalis X which enters the muscle ventrally.

Function: As its name implies it dilates the larynx and opens the glottis.

M. constrictor laryngis (Edgeworth) (m.c.l.).

Constrictor aditus laryngis Henle (1839); Fischer (1843); Drüner (1901).

Ring of Periarytenoideus dorsalis et ventralis . Wilder (1892-6)

Sphincter laryngis Göppert (1894-8).

A small but powerful muscle which surrounds the larynx immediately ventral to the glottis. The shape of the whole muscle is much like a napkin ring. The fibres do not pass right round the circle, however, but are interrupted in the middle line, both dorsally and ventrally, by strong tendinous inscriptions. Most of the muscle fibres arise from, and are inserted into, these inscriptions, but a few of the inner ones have both their origin and insertion confined to the *pars laryngea* of the *cartilago lateralis* which the muscle surrounds. The normal direction of the fibres is somewhat oblique so that their ventral ends are anterior to their dorsal ends, but not infrequently a small bundle may be found which reverses this order, the ventral ends of its fibres being posterior to their dorsal ends, so that the fibres of this bundle cross those of the main mass. Drüner calls them *Fibrae cruciatae*. The M. constrictor laryngis is always relatively a more powerful muscle in the adult than in the larva, and is normally

the only one of the MM. laryngei of the larva which persists to the adult stage. The M. laryngeus ventralis may, however, be represented by a few fibres passing from the lateral end of the lig. dorso-laryngeum to the ventral inscription of the M. constrictor laryngis (Drüner, 1901, p. 532).

Innervation: From the R. recurrens n. intestinalis X.

Function: It constricts the larynx, closes the glottis, and is the antagonist of the M. dilatator laryngis.

6. Muscles of the Head supplied by Spinal Nerves (Pl. VI, figs. 37 and 38).

M. genio-hyoideus (m.g.hy.), Carus (1828); Fischer (1843); Mivart (1869); Osawa (1902).

Rectus lingualis	Funk (1827).
Levator maxillae inferioris s. Geniothyroideus	v. Siebold (1828).
Genio-sous-hyoïdien	Dugès (1834).
Genio-hyoïdien	Cuvier (1835); Rusconi (1854).
Genio-hyoidei-mandibularis	Stannius (1854-6).
Levator maxillae inferioris longus	Schmidt, Goddard, and van d. Hoeven (1864).
Genio-branchial	Humphry (1872).
Maxillo-hyoideus (genio-hyoideus)	Hoffmann (1873-8).
Genio-hyoideus s. rectus superficialis hypobranchialis anterior	

Drüner (1901).

After removing the skin from the floor of the mouth and throat, and turning back the MM. intermandibularis and interhyoideus a pair of strong longitudinal muscles are exposed—they are the MM. genio-hyoidei. They may be regarded as arising from the inner edge of the lower jaw immediately lateral to the origin of the M. genio-glossus, and then, passing backwards and mesialwards, the fibres from either side become very closely approximated in the middle line as they continue their course backwards. The right and left halves of the muscle may remain distinct, but there is often some crossing over and mingling of the fibres. In the larva the muscle is inserted on the posterior end of the uro-branchial cartilage, and in the adult the bulk of the muscle remains attached to the vestige of this cartilage, the *os triangulare*, but some fibres spread to a tendinous inscription which extends in a transverse plane from the lateral extremities of this bone. In addition a small bunch of the most lateral fibres are inserted on the capsule of the thyroid gland. There is, however, some considerable variation in the exact relations of the muscle at its insertion.

Innervation: The hypoglossal nerve traverses the muscle on its way to the tongue, and, in doing so, supplies it with numerous fine twigs.

Function: The muscle may act in several different ways. It may depress the lower jaw, or the whole head, or it may pull forwards the *os triangulare* with its attached truncus arteriosus and heart according to which other muscles are acting in conjunction, or in opposition.

M. genio-hyoideus tertius (Drüner).

Drüner (1901), p. 533, describes what he calls an abnormality of the *M. genio-hyoideus*, in which a few of the most lateral fibres of the muscle on the right side, instead of passing from the jaw to the *os triangulare*, pass from the jaw to the posterior end of the ceratobranchial 1, and lateral to the *M. subarcualis rectus*₁ (*ceratohyoideus internus* of Drüner), which in this case was weaker than the corresponding muscle on the left. He illustrates the muscle in Fig. 24 and there labels it *geniohyoideus tertius*. The innervation is by fine fibres from the hypoglossal nerve.

Another case very similar to Drüner's has been observed in which a muscle, apparently rather smaller than Drüner's, passed from the posterior cornu of the hyoid to the anterior part of the lower jaw. It was also innervated from the N. hypoglossus.

It is interesting in this connexion to refer to the discussion given on p. 59 regarding the homology of the *M. subhyoideus*, since it seems not unreasonable to suggest that the abnormal muscle just described may represent the muscle occurring normally in *Spelerpes*, and described by Miss Louise Smith as the *M. genio-hyoideus lateralis*.

M. genio-glossus (m.g.gl.) Siebold (1828); Fischer (1843); Mivart (1869); Drüner (1901).

Genio-hyoidei Funk (1827).

A fairly strong and somewhat extensive muscle in the Salamander, having a fleshy origin from the mandibular symphysis. After removing the *M. intermandibularis* the genio-glossus muscle may be seen as two triangular blocks filling the angle of the 'chin', but it is necessary to remove both the *M. genio-hyoideus* and the cerato-hyal cartilages before the whole muscle is revealed. It is then seen to consist of two portions: (i) a mesial portion—which is the genio-glossus in the true sense—consisting of more or less parallel fibres passing on either side of the middle line to become inserted in the root of the tongue and in a tough ligament connecting the tongue with the copula—the *aponeurosis lingualis* (Drüner)—and with the

insertion of the *M. rectus cervicis profundus*; (ii) a second portion in which the fibres spread out, more or less fan-shaped, over the floor of the mouth, into which they are inserted at the sides of the tongue.

Innervation: By the terminal twigs of the N. hypoglossus.

Function: The contraction of this muscle must necessarily produce several results according to circumstances. For example, if the tongue were at rest then the muscle would tend to draw it towards the front of the mouth and to arch the dorsal surface, but if the tongue were fully extruded then the contraction of the muscle would tend to retract it towards the mouth. Probably its main function, however, is to compress the glandular tissue of the tongue. This it would do by drawing the tongue towards the front of the mouth under the circumstances first mentioned, and the muscle would thus act as a preliminary for the extrusion of the tongue by causing it to be coated with a sticky mucus to which the prey may adhere.

M. hyoglossus (m.hy.gl.) Fischer (1843); Drüner (1901).

In *Salamandra* this is a small and comparatively unimportant muscle. Its fibres pass from the dorsal side of the anterior extremity of the copula in a posterior direction, on either side of the cartilage. It lies dorsal to the anterior radials (hypohyals) and some fibres also pass dorsal to the posterior radials to be inserted in the tongue, but the more ventral fibres are attached to these cartilages. Drüner distinguishes the ventral fibres as the *M. basiradialis*. The whole muscle lies deep to the *M. rectus cervicis profundus*, which must therefore be removed to expose it. According to Drüner the muscle does not exist in the larva.

Innervation: By terminal twigs from the N. hypoglossus.

Function: Beyond attaching the hyobranchial apparatus securely to the tongue, and possibly assisting to compress the glands of the latter organ, it is difficult to see what useful purpose the muscle can serve. The basi-radial portion would tend to draw the posterior radials antero-dorsally, and thus cause the tongue to stand up from the floor of the mouth as well as to compress the mucus glands.

M. rectus cervicis (Edgeworth).

Pubio-hyoidien s. Pubio-glosse (partim)	. . .	Cuvier (1800).
Hyoideo-ypsiloideus	. . .	Funk (1827).
Sternohyoidien	. . .	Dugès (1834); Rusconi (1854).
Sternohyoideus	Fischer (1843); Owen (1866); Mivart (1869); Humphry (1872); Fürbringer (1873); Walter (1887); Osawa (1902).	

Levator maxillae inferioris brevis	Schmidt, Goddard, and van d. Hoeven (1864).
Thoracico-hyoideus	Hoffmann (1873-8).
Rétracteur de l'hyoide	Perrin (1892).

This muscle represents the direct forward continuation of the *M. rectus abdominis*, as Cuvier's name indicates, and, like that muscle, it is divisible into two strata, one superficial and the other deep. These two layers will be dealt with separately.

M. rectus cervicis superficialis (Edgeworth) (m.r.c.').

Rectus	v. Siebold (1828).
Sterno-hyoideus superficialis	Fürbringer (1873).
Rectus superficialis hypobranchialis s. Sterno-hyoideus	Drüner (1901).

With *M. rectus abdominis superficialis* =

Abdominis musculus rectus (8)	Carus (1828).
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The superficial stratum of the *M. rectus cervicis* may be regarded as arising from the sternum and from the transverse inscription contiguous to it. It passes anteriorly, dorsal to the coracoids and ventral to the pericardium, as a broad thin sheet of muscle. It has at least three insertions: (i) at the angle formed by the hypobranchial 1 with the copula; (ii) on the tendon of insertion of the profundus portion of the muscle by a small deep bundle. The above-mentioned insertions apply only to the more lateral portions of the muscle; the mesial fibres are attached (iii) to the os triangulare and to the inscription from which the *M. genio-hyoideus* arises. Between the sternum and the hyobranchial skeleton there are two transverse tendinous inscriptions, and at the anterior of these the *M. pectoriscapularis* is inserted. It is very closely attached to the pericardium (see also p. 270).

Innervation: The muscle is supplied by twigs from each of the first three spinal nerves.

Function: The mesial fibres support the *M. genio-hyoideus*, while the lateral fibres assist the rectus cervicis profundus in retracting the tongue.

M. rectus cervicis profundus (Edgeworth) (m.r.c.'').

Hebosteoglossus	v. Siebold (1828).
Sterno-hyoideus profundus	Fürbringer (1873).
Rectus hypobranchialis profundus s. Abdomino-hyoideus	Drüner (1901).

With *M. rectus abdominis profundus* =

<i>M. epischio-hyoideus</i> (7)	Carus (1828).
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As already indicated, this muscle forms the direct forward continuation of the *M. rectus abdominis profundus*, so that it is a moot point to speak of its 'origin'. By analogy with the superficial portion it is

perhaps best to regard it as arising at about the level of the sternum. The muscle passes forwards around the lateral parietes of the pericardium, mesial to the thyroid gland, and between the hypobranchial cartilages 1 and 2, passing ventral to the latter and dorsal to the former. It is inserted on the dorsal side of the apex of the copula by means of a strong tendon. The section of the muscle alongside the pericardium passes through a sort of 'sleeve' of connective tissue, so that its contraction does not affect the surrounding structures. Within this 'sleeve', a short distance posterior to the os triangulare, a small bundle of fibres separates from the main mass and loops round mesialwards so to become attached to the *antero-dorsal* aspect of the os triangulare. This bundle was seen by v. Siebold as early as 1828, and was named by him *M. hebosteoypsiloideus*, while it may represent the muscle referred to by Carus as the *oblique epischio-hyoideum* (9).

Innervation: As in the superficial portion; see above.

Function: To retract the tongue or to depress the head, according to circumstances.

M. pectori-scapularis (Edgeworth) (m.p.s.).

Schulterzungenbeinmuskul (omohyoideus) Meckel (1828).

Omo-hyoideus v. Siebold (1828); Rusconi (1854); Mivart (1869);
Humphry (1872); Hoffmann (1873-8); Osawa
(1902).

Scapulo-post-hyoïdien Dugès (1834).

Pectori-scapularis internus Fürbringer (1873).

Pectori-scapularis s. omo-hyoideus Walter (1887); Drüner (1901).

A small, relatively weak, spatulate muscle arising from the mesial aspect of the ventral end of the scapula and inserted, as mentioned above, at the lateral edge of the superficial portion of the *M. rectus cervicis* at the level of the anterior inscriptio tendinea.

Innervation: By a fine twig arising from the R. communicans between the first and second spinal nerves.

Function: The muscle acts as a brace to the *M. rectus cervicis superficialis*.

MUSCLES OF THE FORE-LIMB AND SHOULDER

I. Historical.

The earliest author to make a special study of this region of the body was Rüdinger (1868), whose classic account of the comparative anatomy of the muscles of the neck, shoulder, and fore-limb in Amphibia, Reptiles, Birds, and Mammals is quite well known. This

account was followed some five years later by the more extensive and even better known work of Fürbringer (1873). Although Fürbringer's work is more extensive as regards the range of types studied, it is more limited than Rüdinger's in respect of the *area* investigated, since Fürbringer does not deal with the muscles of the fore-arm and hand. Nevertheless his work shows a considerable advance over that of previous authors in that he deals with the nerves as well as the muscles, and it represents the real starting-point of all subsequent investigations. Both his text and his figures are reproduced by Hoffmann (1873-8). In 1895 Eisler published a long treatise on the homology of the muscles of the tetrapod extremities. His work is not of great importance so far as the Salamander itself is concerned, but is fundamental with regard to the wider question of muscle morphology. The next worker of note is Perrin (1893-9), who has made a detailed study of the muscles of both fore- and hind-limbs in the Amphibia, both Anura and Urodela, Salamandra being taken as the main type of the latter. He makes a useful comparison between the muscles of the anterior and posterior limbs, but his work suffers from the rather serious defect that he has not studied the nerves in conjunction with the muscles, and hence his groupings are sometimes a little unfortunate. The work of McMurrich (1903), although not of specific importance so far as Salamandra is concerned, is nevertheless relevant from a phylogenetic point of view. His conclusions are discussed in the text. A comparative account of the extensor muscles and their nerves in both fore- and hind-limbs of Urodeles was given by Sieglbaur in 1904, but no mention is made of the condition on the flexor side of the limbs. The muscles and nerves of the distal portions of the limbs of Amphibia, Reptiles, and Mammals have been adequately dealt with by Ribbing (1907-9). His account is clear and critical, and both his terminology and grouping have been adopted here. More recently (1924) Hellen Rylkoff has studied the development of the shoulder-muscles of Salamandra and finds that they are divisible into two main groups, namely, the *primary shoulder muscles* which develop from the humerus towards the shoulder-girdle, and the *secondary shoulder muscles* which develop *centrifugally* towards the limb. The former group is again divisible into a dorsal and a ventral group. The dorsal primary group comprises the M. anconaeus, the M. dorso-humeralis,¹ the M. dorsalis scapulae, and the dorsal part of the M. procoraco-humeralis, while the ventral primary group consists of the M. humero-

¹ The names here given are those used in this work; Rylkoff's synonyms may be found by consulting the lists preceding the description of each muscle.

antibrachialis inferior, the M. pectoralis, the MM. coraco-brachialis longus and brevis, the M. supra-coracoideus, and the ventral part of the M. procoraco-humeralis. The dorsal and ventral groups may be further subdivided by a vertical plane into anterior and posterior elements. The secondary muscles of the shoulder-girdle are the MM. thoraci-scapularis, developing from the trunk myotomes 2-5, the M. opercularis, which develops from the trunk myotomes 1-2, and the M. cucullaris which arises from the visceral myotomes.

2. Shoulder-muscles (Pl. VII, fig. 43).

M. opercularis (m.o.). Gaupp (1898); Kingsbury and Reed (1909).

Levator anguli scapulae . . . Funk (1827); Rüdinger (1868);
Mivart (1869).

Levator scapulae Carus (1828); Schmidt, Goddard, and van d.
Hoeven (1864); Humphry (1871); Osawa (1902);
Rylkoff (1924).

Sous-occipito-adscapulaire (32). . . . Dugès (1834).

Fasciculus of protractor scapulae . . . Owen (1866).

Basi-scapularis (levator scapulae) . . . Fürbringer (1873).

Basi-scapularis (levator scapularis) . . . Hoffmann (1873-8).

Protracteur du scapulum (98) . . . Perrin (1899).

Levator scapuli . . . Drüner (1901).

This peculiar muscle has a fleshy origin from the cartilaginous operculum of the ear capsule. It passes directly backwards alongside the dorsal trunk-muscles of the neck region, mesial to the M. cucullaris and to the ninth and tenth cranial nerves, and is inserted along the anterior border of the cartilaginous suprascapula. It is practically circular in section at its origin, but spreads out fan-shaped at its insertion. It is a derivative of the M. levator scapulae, and was first named M. opercularis by Gaupp. It seems better to retain Gaupp's name for the muscle in the Salamander owing to its peculiar origin and function.

Innervation: By one or two fine twigs from the first spinal nerve—N. hypoglossus.

Function: The function of this muscle is more fully discussed in the section dealing with the auditory organ (p. 295), but, in addition to acting as a track for auditory impulses, a tension on the muscle would tend to 'damp out' the effect which would be produced by the inertia of the operculum at every sudden movement of the head. For these functions alone the muscle seems surprisingly powerful, but in view of the lack of any direct experimental evidence it is unsafe to speculate further.

M. cucullaris (Edgeworth) (m.c.). Rylkoff (1924).

Omo-mastoideus	Funk (1827).
Vorwärtszieher der Schulter	Meckel (1828).
Levator scapulae (<i>partim</i>) (20)	Carus (1828).
Spini-sus-scapulaire, portion du trapèze, masto-sus-acromial ou sterno-mastoidien, ex-occipito-sus-scapulaire (28, 29, 30, 31)	Dugès (1834).
Fasciculus of Protractor scapulae	Owen (1866).
Cucullaris et Sterno-cleido-mastoideus	Rüdinger (1868).
Trapezius	Mivart (1869); Humphry (1872); Drüner (1901); Osawa (1902).
Capiti-dorso-scapularis s. Cucullaris	Fürbringer (1873); Hoffmann (1873-8).
Petroso-dorso-scapularis (96-7)	Perrin (1899).

A thin triangular sheet of muscle which arises by two heads. The posterior, or *cucullaris minor*, arises from the *fascia cephalodorsalis*, and is consequently firmly attached to the skin. Its fibres run directly ventralwards and it passes mesial to the anterior portion towards its insertion, which is on the lateral border of the pro-coracoid and scapula. The fibres are nearly parallel, converging slightly towards their insertion. The anterior portion, or *cucullaris major*, arises partly from the *fascia cephalodorsalis*, but chiefly from the postero-dorsal surface of the skull and from a raphe which occurs between this portion of the muscle and the *M. depressor mandibulae*. It has a fleshy insertion on the lateral face of the pro-coracoid near the shoulder-joint, while a few of the posterior fibres are attached to the anterior edge of the ventral end of the scapula. The *cucullaris major* is triangular in shape, the anterior fibres being very oblique, while the posterior fibres are nearly vertical. The antero-ventral edge of the muscle is considerably thicker than the postero-dorsal. Although the *M. cucullaris* is essentially a superficial muscle it lies deep to the *M. depressor mandibulae* anteriorly, as well as to the *MM. cephalo-dorso-subpharyngeus* and *dilatator laryngis*, it being necessary to remove, or turn back, these muscles in order to expose it fully. Its insertion is on the adjoining parts of the pro-coracoid and scapula between the *M. dorsalis scapulae* and the *M. procoraco-humeralis*. Carus (1828) labels a muscle *M. scapulare-cutaneus* which is apparently identical with the *cucullaris minor*.

Innervation: From N. accessorius X which enters its mesial surface. The *cucullaris minor* also receives a twig from the N. thoracicus superior 2 (second spinal nerve).

Function: The muscle must be mainly responsible for turning or depressing the head according to circumstances. If the head were

held firm by the dorsal trunk muscles then it would protract the pectoral girdle.

M. dorsalis scapulae (m.d.s.). Humphry (1872); Rüdinger (1868); Fürbringer (1873); Hoffmann (1873-8); Osawa (1902).

Sur-épineux et Sous-épineux conjoints	Cuvier (1800).
Scapularis	Funk (1827).
Auswärtszieher oder oberer äusserer Schulterblattmuskel		Meckel (1828).
(?) Externus (supra—et infra—spinatus) et internus scapulae (subscapularis) (22)	Carus (1828).
Adscapulo-huméral, sous-épineux	Dugès (1834).
Suprascapularis	Stannius (1854-6); Rylkoff (1924).
Subscapularis	Schmidt, Goddard, and van d. Hoeven (1864).
Supra- and infra-spinatus, and perhaps also Deltoideus		Owen (1866).
Deltoid	Mivart (1869).
Élévateur scapulaire du bras (90)	Perrin (1899).

This muscle is fan-shaped and arises from the dorso-lateral surface of the cartilaginous suprascapula, and is partly covered by the *M. dorso-humeralis*. Its fibres run ventralwards and converge to a very strong tendon which is inserted on the side of the crista ventralis humeri. This insertion lies between those of the *M. procoraco-humeralis* and the *M. dorso-humeralis*, but is entirely separate from both.

Innervation: By the N. dorsalis scapulae from the third spinal nerve.

Function: Its function is obviously to raise the arm in a vertical plane passing through the shoulder-joint.

M. dorso-humeralis (m.d.h.).

Grand dorsal	Cuvier (1800).
Oberer Rückwärtszieher oder breiter Rückenmuskel		Meckel (1828).
Latissimus dorsi	Funk (1827); Carus (1828); Stannius (1854-6);
		Schmidt, Goddard, and van d. Hoeven (1864);
		Owen (1866); Rüdinger (1868); Mivart (1869);
		Humphry (1872); Osawa (1902); Rylkoff (1924).
Vertébro-costo-huméral, grand dorsal	Dugès (1834).
<i>M. dorso-humeralis</i> (latissimus dorsi)		Fürbringer (1873); Hoffmann
		(1873-8).
Élévateur dorsal du bras (89)	Perrin (1899).

A large, flat, triangular muscle plate, situated behind the shoulder, which takes its origin from the dorsal fascia continuous with that from which the *M. cucullaris* and *M. depressor mandibulae*, &c.,

arise—the *fascia cephalodorsalis*. The fibres are closely connected with the skin dorsally, and with the tendinous inscriptions of the body-muscles mesially. The origin of the muscle extends backwards over about three to four vertebrae, while its anterior border partially overlies the M. dors. scap. The fibres converge very strongly, the anterior ones being nearly vertical and the posterior ones very oblique. At the shoulder-joint they pass into a very strong, flat tendon which has two insertions. The first is at the postero-lateral edge of the shoulder-joint, where it merges into the tendon of origin of caput *a* (scapularis medialis) of the M. anconaeus. The second insertion is on the antero-lateral border of the humerus, just behind that of the M. dors. scap. The tendon of this latter insertion is very long and strong, and passes mesial to the M. dors. scap., forming a sort of tendinous bridge over the articulation.

Innervation: By the N. dorso-humeralis which emerges from an anastomosis of the third and fourth spinal nerves. It enters the anterior border of the muscle.

Function: It is the retractor of the humerus, and opposes the M. procoraco-humeralis.

The three muscles just described are all *dorsal* shoulder-muscles and are *lateral* to the scapula. The one now to be considered also lies *dorsal* to the shoulder-joint but *mesial* to the scapula.

M. thoraci-scapularis (serratus magnus). Fürbringer (1873); Hoffmann (1873-8).

Depressor anguli scapulae inferioris	Funk (1827).
Serratus anticus magnus (21)	Carus (1828).
Grosser Rückwärtszieher der Schulter	Meckel (1828).
Costo-sous-scapulaire, ou grand dentelé	Dugès (1834).
Levator scapulae et serratus anticus major	Owen (1866).
Serratus anticus magnus	Rüdinger (1868).
Serratus magnus	Mivart (1869); Humphry (1872).
Rétracteur du scapulum (99, 100)+Suspenseur scapulaire (101)	Perrin (1899).
Thoraci-superiores-serrati	Rylkoff (1924).

This muscle consists of a series of bundles arising from the first five ribs, which are inserted on the mesial face of the scapula. Fürbringer divides it into two sections, an 'Obere Partie' and an 'Untere Partie', while Perrin distinguishes two distinct muscles (see above), the former of which he again subdivides into two sections. Perrin's grouping has been retained here, but it seems preferable to regard his 'M. rétracteur du scapulum' and 'M. suspenseur scapulaire' as

'oblique' and 'straight' portions respectively, of a common muscle, since the innervation is virtually the same in each case.

The *straight portion* consists of two flat sheets of muscle arising from the lateral faces of the expanded ends of the first two ribs. The fibres pass directly dorsalwards and are inserted on the dorso-mesial border of the suprascapula.

Innervation: From the NN. thoracici superiores of the second, third, and fourth spinal nerves.

Function: The muscles serve to depress the scapula and thus cause the ventral portion of the pectoral girdle to expand.

The *oblique portion* again consists of two sections. The anterior of these arises from the lateral face of the second rib, just ventral to the straight portion. It passes anteriorly, inclined slightly dorsalwards, and is inserted on the antero-mesial border of the suprascapula. The second portion arises by three heads from the third, fourth, and fifth ribs. These unite into a single bundle passing antero-dorsally to be inserted on the postero-dorsal angle of the suprascapula. This portion of the muscle lies deep to the M. dorso-humeralis.

Innervation: As above.

Function: It serves to retract the scapula, while the general function of the M. thoraci-scapularis as a whole is to attach the pectoral girdle to the axial skeleton, thus forming an elastic suspension for the anterior part of the body.

The muscles associated with the ventral half of the pectoral girdle are all inserted in the limb, and are therefore considered in the sections which follow (Pl. VII, figs. 43 and 45).

3. Muscles of the Arm.¹

M. pectoralis (m.p.). Schmidt, Goddard, and van d. Hoeven (1864); Owen (1866); Mivart (1869); Humphry (1872); Fürbringer (1873); Hoffmann (1873-8); Rylkoff (1924).

Grand pectoral Cuvier (1800).

Portio inferior m. pectoralis majoris Funk (1827).

Grosser Brustmuskel Meckel (1828).

Abdomino-coraco-huméral, portion du grand pectoral Dugès (1834).

Pectoralis major Stannius (1854-6); Rüdinger (1868).

Pectoralis sternalis + pectoralis abdominalis Eisler (1895).

Tête sternale; fléchisseur du bras (86) Perrin (1899).

Together with MM. supracoracoideus and procoraco-humeralis =

Pectoralis magnus + Pectoralis magnus, pars anterior Carus (1828).

¹ As in the case of the skeleton the proximal joint of the limb is referred to as the 'arm', and the distal joint as the 'fore-arm'.

The *M. pectoralis* is a large, superficial, fan-shaped plate of muscle covering the posterior region of the breast. Its anterior fibres are approximately transverse to the vertebral axis and gradually become more and more oblique until eventually the posterior ones are almost longitudinal. The muscle has a varied origin. Anteriorly the fibres lying ventral to the coracoid arise from a median aponeurosis separating the muscles of the right and left sides, next a few fibres arise from the sternal plate, then follows a section which takes its origin from the wide aponeurosis of the *M. obliquus externus superficialis*, and finally the most posterior fibres of all are continuous with those of the *M. rectus abdominis superficialis*. All the fibres converge to a strong tendon, which is inserted, together with that of the *M. supra-coracoideus*, on the posterior aspect of the *crista ventralis humeri*.

Innervation: By the *N. pectoralis* which arises from the fourth (or fourth and fifth) spinal nerve and enters the posterior portion of the muscle on its mesial aspect.

Function: To draw the arm inwards towards the body and posteriorly, or if the hand is resting on the ground, to advance the body.

MM. supracoracoideus and *coraco-radialis proprius*. Fürbringer (1873); Hoffmann (1873-8); Osawa (1902).

These two muscle slips are very difficult to separate, and in fact their separation must be regarded as largely artificial, while they are most clearly distinguished by their insertions.

(a) *M. supracoracoideus* (m.s.c.). Osawa (1902); Rylkoff (1924).

Portio media m. pectoralis majoris	Funk (1827).
Einwärtszieher, Theil des grossen Brustmuskels	Meckel (1828).
Clavi-huméral, portion du grand pectoral	Dugès (1834).
Pectoralis secundus	Stannius (1854-6).
Pectoralis minor Schmidt, Goddard, and van d. Hoeven	(1864).
Part of pectoralis	Owen (1866).
Coraco-brachialis proprius	Rüdinger (1868).
First part of coraco-brachialis	Mivart (1869).
Epicoraco-humeral	Humphry (1872).

The more superficial of the two slips arises from the ventral surface of the cartilaginous portion of the coracoid, with the exception of the posterior third. Its fibres converge to a flat tendon, which is inserted, together with that of the *M. pectoralis*, on the posterior face of the *crista ventralis humeri*. The posterior half of the muscle is covered by the *M. pectoralis*.

(b) *M. coraco-radialis proprius*. Stannius (1854-6).

Biceps brachii	Rüdinger (1868).
Part of biceps	Mivart (1869).
Coraco-radialis or biceps	Humphry (1872).
Long fléchisseur de l'avant-bras (85)	Perrin (1899).
Coraco-radialis	Osawa (1902).

This section of the muscle also arises from the ventral surface of the coracoid, deep to the foregoing slip. It is a very thin, fan-like muscle and converges, at the glenoid cavity, to a strong two-lipped tendon. The shorter lip is inserted close to that of the former slip on the flexor side of the head of the humerus, while the longer tendon (m.c.r') passes right down the arm, lying parallel with the humerus, and between the *M. coraco-brachialis longus* and the *M. humero-antibrachialis*. It is inserted on the mesial aspect of the proximal end of the radius.

Innervation: Both slips are innervated by the N. supracoracoideus, from the second and third spinal nerves.

Function: Both muscles serve to draw the arm towards the body, while the tendon of the latter portion also assists in flexing the elbow. In general it is the opposer of the *M. dors. scap.*

M. procoraco-humeralis (m.p-h.). Fürbringer (1873); Hoffmann (1873-8); Osawa (1902); Rylkoff (1924).

Portio superior m. pectoralis majoris	.	.	.	Funk (1827).
Vorwärtszieher oder Heber des Oberarms, dreieckiger Muskel	.	.	.	Meckel (1828).
Acromio-huméral, Deltoïde	.	.	.	Dugès (1834).
Deltoides	.	.	.	Stannius (1854-6); Rüdinger (1868).
Subclavius	.	.	.	Mivart (1869).
Precoraco-brachial	.	.	.	Humphry (1872).
Adducteur inférieur du bras (92)	.	.	.	Perrin (1899).

This muscle arises from the pro-coracoid portion of the pectoral girdle, and passes posteriorly to be inserted on the head of the humerus. The tendon of insertion is attached to the humerus a little antero-mesial to the insertion of the *M. dorsalis scapulae*, while a few fibres may be inserted between this muscle and the anterior insertion of the *M. dorso-humeralis*. The shape of the muscle is that of a narrow fan.

Innervation: The muscle has a dual innervation. At its lateral border it receives a branch from the N. dorsalis scapulae, and at its mesial border it is supplied by the N. supracoracoideus.

Function: If the foot is raised from the ground the contraction of

the muscle tends to draw the limb forwards and at the same time to turn the humerus so as to depress the pre-axial side of the limb. If, however, the foot is resting on the ground this tendency to twist the humerus would assist in propelling the body forwards.

MM. coraco-brachialis longus et brevis. Humphry (1872); Fürbringer (1873); Hoffmann (1873-8); Osawa (1902); Rylkoff (1924).

Hakenarmmuskeln. Meckel (1828).

Coraco-huméral Dugès (1834).

Coraco-brachialis . Stannius (1854-6); Rüdinger (1868); Schmidt, Goddard, and van d. Hoeven (1864).

Second part of coraco-brachialis Mivart (1869).

Coraco-brachialis longus, superficialis, and brevis Eisler (1895).

(supracoracoideus + coraco-brachialis brevis) =

Tête coracoïdienne; fléchisseur du bras (87) Perrin (1899).

(coraco-brachialis longus) =

Déducteur du bras (88) Perrin (1899).

The *caput longum* (m.c.b.l.) is a muscle of medium power covering the posterior face of the humerus. It arises from the postero-lateral border of the coracoid a little towards its dorsal side. Its fibres run parallel with one another and with the humerus, and have a fleshy insertion along the posterior surface of the distal half of this bone.

The *caput breve* is a short but powerful triangular muscle, separated from the former head by the N. brachialis. It arises from the posterior third of the ventral surface of the coracoid, i.e. posterior to the M. supracoracoideus, and also from the postero-lateral edge—lateral to the head just described—and encroaches a little on the dorsal and mesial sides of the coracoid. It is inserted on the posterior face of the proximal half of the humerus, and immediately proximal to the *caput longum*.

Innervation: By the NN. coraco-brachiales from the R. superficialis, N. brachialis.

Function: Both heads serve to draw the arm caudalwards, or conversely, if the foot is resting on the ground to propel the body forwards.

M. subscapularis. Funk (1827); Stannius (1854-6); Rüdinger (1868); Mivart (1869); Osawa (1902).

Sous-scapulo-huméral, sous-scapulaire Dugès (1834).

Coraco-brachialis quartus (subscapularis) Humphry (1872).

Subcoracoscapularis . Fürbringer (1873); Hoffmann (1873-8); Rylkoff (1924).

Subscapularis (dorsal portion) Subcoracoscapularis Eisler (1895).

Adducteur supérieur du bras (93 and 94) Perrin (1899).

A muscle of medium strength arising from the dorsal surface of the pro-coracoid. The fibres pass caudalwards to the posterior margin of the coracoid where they turn sharply round lateralwards, and are inserted on the *crista dorsalis humeri*. The M. anconaeus coracoideus, and the MM. coraco-brachialis longus et brevis lie on the ventral side, and the M. anconaeus scapularis medius is on the dorsal side of this muscle.

Innervation: By the N. subscapularis from the third spinal nerve.

Function: The contraction of the muscle draws the arm backwards and thus, if the foot is resting on the ground, it serves to advance the body.

M. anconaeus. Fürbringer (1873); Hoffmann (1873-8); Rylkoff (1924); Osawa (1902).

Anconaeus internus et externus	Funk (1827).
Triceps brachii extensor (24)	Carus (1828).
Strecker des Vorderarms	Meckel (1828).
Scapulo-huméro-olécraniens, triceps	Dugès (1834).
Streckmuskelmasse	Stannius (1854-6).
Triceps brachii s. anconaeus	Rüdinger (1868); Mivart (1869).
Triceps and coraco-olecranalis	Humphry (1872).
Extenseur de l'avant-bras (81-3)	Perrin (1899).

The M. anconaeus arises from the shoulder-girdle and humerus by four heads which unite distally, to a greater or lesser extent, to form a powerful muscle which is inserted on the olecranon process of the ulna. In general it is *innervated* by the extensor nerves, and *functions* as extensor of the fore-arm. The details of its several components may be considered separately.

Caput (*a*). *M. anconaeus scapularis medialis* (m.a.s.m.). Fürbringer (1873); Hoffmann (1873-8); Rylkoff (1924).

Anconaeus longus	Eisler (1895).
Tête antérieur (81)	Perrin (1899).
Anconaeus caput scapulare	Osawa (1902).

This head arises from the scapula at the posterior margin of the glenoid cavity. The main tendon arises a little towards the *mesial* side of the scapula, but retains a strong fibrous connexion with the whole posterior region of the capsule surrounding the joint. The muscle is thin and flat, and is separated from the M. anconaeus coracoideus by the entry of the extensor nerves and the V. brachialis medialis into the arm, as well as by the insertion of the M. subscapularis.

Innervation: By twigs from the N. extensorius caudalis (cf. p. 166).

Function: See above.

Caput (*b*). *M. anconaeus coracoideus* (m.ac.c.). Fürbringer (1873); Hoffman (1873-8); Eisler (1895); Rylkoff (1924).

Coraco-olecranonalis	Humphry (1872).
Tête postérieur (82)	Perrin (1899).
Anconaeus caput coracoideum	Osawa (1902).

This portion of the anconaeus muscle arises by a long, tough tendon from the mesial surface of the bony portion of the coracoid. It is relatively small and slight, and joins the former muscle at about the middle of the humerus. As already mentioned it is separated from the head just described by the extensor nerves and by the insertion of the *M. subscapularis*.

Innervation: As caput (*a*). See above.

Function: See above.

Caput (*c*). *M. anconaeus humeralis lateralis* (m.a.h.l.). Fürbringer (1873); Hoffmann (1873-8); Rylkoff (1924).

Anconaeus caput humerale mediale	Osawa (1902).
With caput <i>d</i> = Tête profonde (83)	Perrin (1899).

Situated on the dorso-lateral surface of the arm the *M. anconaeus humeralis lateralis* is considerably larger than the two portions of the anconaeus muscle already described. It arises from the proximal third of the antero-lateral surface of the humerus, just posterior to the insertions of the *MM. dorso-humeralis* and *dorsalis scapulae*. The direction of its fibres is at first approximately parallel with the humerus, but distally they become oblique in an antero-posterior direction, and the whole muscle passes over to join the other heads on the extensor surface of the arm. It is separated from the head next to be described by the extensor nerves.

Innervation: By twigs from both extensor nerves.

Function: See above.

Caput (*d*). *M. anconaeus humeralis medialis* (m.a.h.m.). Fürbringer (1873); Hoffmann (1873-8); Rylkoff (1924).

Anconaeus caput humerale laterale	Osawa (1902).
With caput <i>c</i> = Tête profonde (83)	Perrin (1899).

The fourth head of the anconaeus takes its origin from the whole extensor surface of the humerus. It lies mesial to the *scapularis* and *coracoideus* portions of the muscle and joins them distally near the common insertion.

Innervation: From the *N. extensorius cranialis*.

Function: See general account of whole muscle.

M. humero-antibrachialis (m.h.a.). Rylkoff (1924).

Brachialis medius	Funk (1827).
Flexor brachii (biceps cum brachiali interno) (23)	Carus (1828).
Oberer Beuger des Vorderarms	Meckel (1828).
Huméro-radial s. biceps	Dugès (1834).
Humero-radialis	Stannius (1854-6); Osawa (1902).
Biceps	Schmidt, Goddard, and van d. Hoeven (1864).
Biceps and brachialis internus	Owen (1866).
Brachialis internus	Rüdinger (1868).
Part of biceps	Mivart (1869).
Brachialis anticus	Humphry (1872); Eisler (1895).
Humero-antibrachialis inferior (Brachialis inferior)	Fürbringer (1873); Hoffmann (1873-8).
Court fléchisseur de l'avant bras (84)	Perrin (1899).

This muscle arises from the flexor side of the humerus, distal to the *crista ventralis humeri*, and runs parallel with the bone, converging slightly towards its distal end. Its insertion on the proximal end of the radius is inclined to become tendinous.

Innervation: It is supplied by one or two branches from the R. superficialis N. brachialis.

Function: It is the true flexor muscle of the elbow.

4. Extensor Muscles of the Fore-arm and Hand (Pl. VII, figs. 43 and 44).

These should be dissected from the dorsal side.

M. extensor digitorum communis (m.e.d.). Rymer Jones (1852); Schmidt, Goddard, and van d. Hoeven (1864); Rüdinger (1868); Ribbing (1907).

Extensor digitorum (30)	Carus (1828).
Gemeinschaftlicher Strecker	Meckel (1828).
Epicondylo-digital	Dugès (1834).
Extensor longus	Mivart (1869).
Extensor digitorum sublimis	Humphry (1872); Rylkoff (1924).
Humero-digiti II-V dorsalis	Hoffmann (1873-8).
Extensor digitorum communis longus	Eisler (1895).
Extenseur de la main (63)	Perrin (1899).
Extensor digitorum longus	Osawa (1902).
Humero-metacarpalis	Sieglbaur (1904).

This is the most superficial muscle on the extensor surface of the fore-arm. It arises by means of a thin, broad tendon from the *epicondylus lateralis humeri*, superficial to the MM. extensor antibrachii et carpi ulnaris and radialis, and spreads out as a flat plate of muscle covering the extensor surface of the fore-arm and wrist. Distally it

separates into six tendons, which are inserted on either side of the bases of the metacarpals of each of the three ulnar fingers. Occasionally a seventh tendon may be present which is then inserted on the post-axial side of the base of the first metacarpal.

Innervation: From the N. dorsalis manus ulnaris, by twigs passing between the extensor muscles of the ulnar and radial sides of the fore-arm.

Function: As its name implies it is the common extensor of the hand.

M. extensor antibrachii et carpi radialis (m.e.a.c.r.). Eisler (1895); Ribbing (1907).

Extensor carpi radialis (28)	Carus (1828).
Gemeinschaftlicher Heber	Meckel (1828).
Epicondylo-carpium; Sus-epicondylo-radial	Dugès (1834).
Extensor carpi radialis	Rymer Jones (1852); Schmidt, Goddard, and van d. Hoeven (1864); Osawa (1902).
Abductor	Stannius (1854-6).
Supinator longus and brevis	Rüdinger (1868).
Supinator	Mivart (1869).
Radial section of the superficial stratum representing the Supinator longus and brevis, and the Extensor carpi radialis	Humphry (1872).
Humero-radialis dorsalis	Hoffmann (1873-8).
Élévateur carpien interne (66); Élévateur du radius (67)	Perrin (1899).

A very powerful muscle, arising from almost the whole surface of the *epicondylus lateralis humeri* and from the strong raphe which occurs between its proximal end and that of the M. ext. ant. et carp. ulnaris. It has a fleshy insertion along the whole length of the lateral surface of the radius with the exception of about a millimetre at the proximal end (= M. ext. ant. rad.), and on the radiale (= M. ext. carp. rad.).

Innervation: Mainly from the N. extensorius cranialis with a few fibres from the N. extensorius caudalis.

Function: In conjunction with the M. ext. ant. et carp. ulnaris and the M. ext. dig. comm. it would act as an extensor muscle. Alone it would tend to turn the hand into the supine position.

M. extensor antibrachii et carpi ulnaris (m.e.a.c.u.). Eisler (1895); Ribbing (1907).

Extensor carpi ulnaris	Carus (1828); Rymer Jones (1852); Schmidt, Goddard, and van d. Hoeven (1864); Humphry (1872); Osawa (1902).
Eigener Heber	Meckel (1828).
Epicondylo-cubital	Dugès (1834).

Extensor carpi	Stannius (1854-6).
Extensor carpi s. metacarpi radialis et ulnaris	Rüdinger (1868).
Humero-ulnaris dorsalis	Hoffmann (1873-8); Rylkoff (1924).
Élévateur cubito-carpien (64-5)	Perrin (1899).
Ulnaris externus	Sieglbaur (1904).

This muscle forms the ulnar counterpart of the foregoing. It arises from the extensor border of the epicondylus lat. hum., and from the raphe mentioned above as occurring between this and the previous muscle. It is inserted along the central portion of the lateral face of the ulna (= M. ext. antibr. ulnaris) and on the ulnare+intermedium (= M. ext. carp. ulnaris).

Innervation: From the N. extensorius caudalis.

Function: It is the true extensor of the fore-arm.

All three of the foregoing muscles are closely associated at their origin. The separation of the two latter muscles into 'antibrachii' and 'carpi' portions is to be regarded as in an incipient state in the Salamander, and varies in different individuals. They are usually separable distally, since the 'antibrachii' portions have fleshy insertions on the radius or ulna, while the 'carpi' portions are gathered into strong tendons before their insertions.

M. abductor and extensor digiti primi (m.a.e.i.). Sieglbaur (1904).

(?) Hallici proprius	Carus (1828).
Cubito-sus-pollicien	Dugès (1834).
Extensores et Adductores	Stannius (1854-6).
Extensor digiti I	Rüdinger (1868).
Extensor brevis	Mivart (1869).
Uppermost part of the deep stratum s. Supinator manus	

Humphry (1872).

Ulnari-phalanx II dorsalis Hoffmann (1873-8).

Abductor metacarpi II + extensor digiti II brevis superficialis

Eisler (1895).

Court adducteur du premier métacarpien (69) + Court extenseur du premier doigt (70 et 71) Perrin (1899).

Abductor digiti secundi + Extensor brevis digiti II Osawa (1902).

This muscle group arises mainly from the combined *ulnare+intermedium*, while a few fibres (possibly representing the M. extensor brevis digiti I profundus?) take their origin from the *os centrale*. It passes obliquely across the wrist and is inserted on the outer edge of the proximal end of the first metacarpal (= M. abductor digiti I), and on the distal end of the same bone (= M. extensor digiti I).

Innervation: From the N. dorsalis manus intermedius.

Function: It is the extensor muscle of the first digit. It would

appear that again this muscle is to be regarded as a case of the incipient separation of two muscles primitively united. The 'abductor' portion probably assists in supination (cf. Ribbing).

MM. extensores breves digitorum (m.e.b.). Ribbing (1907).

Extensor brevis	Carus (1828).
Extensores et adductores	Stannius (1854-6).
Extensor digitorum brevis s. profundus	Humphry (1872).
Carpo-phalangei	Hoffmann (1873-8).
Extensor brevis superficialis digitorum + Extensor brevis profundus digitorum	Eisler (1895).
Courts extenseurs des doigts (72-7)	Perrin (1899).
Extensores digitorum breves s. profundus III-IV	Osawa (1902).
Extensores digitorum II, III, et IV.	Sieglbaur (1904).

These small muscles arise in two layers. The more superficial and thicker stratum takes its origin from the *ulnare* + *intermedium* and the *os centrale* (for the second digit), while the deeper and thinner layer arises from the basal carpalia, each muscle springing from the basal of the corresponding digit. The two strata of the muscle are separated by the branches of the A. perforans carpi. They have a tendency to unite distally into long thin tendons which pass along the extensor surfaces of the fingers and are inserted on the proximal end of each phalanx.

Innervation: From the NN. dorsales manus inter. and ulnaris.

Function: Extensors of the fingers.

M. extensor lateralis digiti quarti (m.e.l.d.4.) (mihi).

Court déducteur du quatrième metacarpien (80) . . . Perrin (1899)

First described by Perrin, this very small muscle arises from the distal external angle of the *ulnare* + *intermedium* and is inserted laterally on the proximal angle of the fourth metacarpal. Its fibres are accordingly very short.

Innervation: From N. dorsalis manus ulnaris.

Function: To assist in extending the hand by drawing the fourth digit laterally. Opposer of the MM. intermetacarpales.

5. Flexor muscles of the Fore-arm and Hand (Pl. VII, figs. 45 and 46).

These should be dissected from the ventral side. They are more numerous than the extensor muscles.

M. flexor primordialis communis (m.f.p.). Ribbing (1807).

Flexor digitorum (29)	Carus (1828).
Palmaris superficialis	Eisler (1895); McMurrich (1903).

Together with MM. flexores breves superficiales and flexores accessorii lateralis and medialis =

Flexor digitorum communis profundus et sublimis Funk (1827).

Langer gemeinschaftlicher Beuger Meckel (1828).

Epitrochlo-digital Dugès (1834).

Flexor digitorum communis Stannius (1854-6); Rymer Jones (1852);
Schmidt, Goddard, and van d. Hoeven
(1864); Rüdinger (1868).

Flexor longus Mivart (1869).

Humero-phalangei volares II-V Hoffmann (1873-8).

Fléchisseur commun des doigts (14-28) Perrin (1899).

Together with MM. flexores breves superficiales, and flexor accessorius lateralis =

Flexor digitorum sublimis Humphry (1872).

Together with MM. flexores accessorii lateralis et medialis =

Flexor digitorum longus sublimis Osawa (1902).

The *flexor primordialis communis* is a thin, flat sheet of muscle arising from the *epicondylus medialis humeri* between the MM. flexor anti-brachialis et carpi radialis and ulnaris and from aponeuroses which occur between it and these muscles. It is very difficult to separate proximally from the flexor carpi ulnaris; indeed, there is no natural division between them other than the common aponeurosis from which their fibres originate. In the region of the carpus the muscle passes into a thin, flat tendon which occupies the whole of the palm of the hand, and then divides into four narrow tendons which pass along the fingers and are inserted on the terminal phalanges, while an auxiliary tendon passes to the second phalanx of the third finger. The tendon is fixed to the skin at the carpus by tough fibrous connective tissue and is also related to various other muscles. See below.

Innervation: From N. ulnaris.

Function: As its name indicates, it is the common flexor of the hand and fingers.

To observe the following muscles the M. flex. prim. comm. should be severed at its *origin* and turned backwards over the hand, care being taken not to damage the short flexor muscles of the wrist which are inserted on the palmar tendon.

M. flexor antibrachii et carpi radialis (m.f.a.c.r.). Eisler (1895);
McMurrich (1903); Ribbing (1907).

Pronator carpi radialis (?) Funk (1827).

Flexor carpi radialis (25) Carus (1828); Osawa (1902).

Abzieher oder Beuger der Hand Meckel (1828).

Sous-epitrochlo-radial	Dugès (1834).
Adductor	Stannius (1854-6).
Pronator teres	Schmidt, Goddard, and van d. Hoeven (1864); Rüdinger (1868); Mivart (1869).
Radial sector of the superficial stratum representing the Pronator teres and the flexor carpi radialis	Humphry (1872).
Humero-radialis volaris	Hoffmann (1875-8).
Abaisseur radio-carpien interne (39-40)	Perrin (1899).

This muscle arises from the *epicondylus medialis humeri* together with the M. flex. prim. comm., from which it is very difficult to separate at the proximal end. It has a fleshy insertion all along the external face of the radius (= flexor antibrachii radialis), while the most external fibres are attached to the radiale (= flexor carpi radialis). The separation of these two strata is not a natural one in Salamandra, since in this animal the muscle—although of medium strength—is relatively weak when compared with other Urodeles (cf. Ribbing).

Innervation: From the N. ulnaris, and from the R. superficialis N. brachialis before it anastomoses with the R. profundus—for details see these nerves, p. 168.

Function: It is a flexor of the fore-arm.

The muscle of the ulnar side of the arm corresponding to the foregoing radial muscle is comparatively easily separated into its components, which may therefore be considered separately.

M. flexor carpi ulnaris (m.f.a.c.u.). Ribbing (1907).

Abductor digiti minimi	Schmidt, Goddard, and van d. Hoeven (1864); Humphry (1872).
Flexor digiti minimi proprius	Rüdinger (1868).
Humero-metacarpus V volaris	Hoffmann (1873-8).
Ulnaris internus	Eisler (1895).
Abaisseur carpien externe (37)	Perrin (1899).

Together with the following muscle =

Flexor carpi ulnaris	Carus (1828); Rymer Jones (1852); Humphry (1872); Osawa (1902).
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The carpal portion is the more superficial of the two strata. It arises partly from the *epicondylus medialis humeri*, but mainly from either side of a strong raphe, from which also some of the fibres of the M. flex. prim. comm. originate. It runs down the ulnar side of the fore-arm and, at the level of the wrist, converges into a strong tendon which is inserted on the lateral face of the ulnare+intermedium, just proximal to the origin of the M. flex. brevis profundus IV.

Innervation: By N. ulnaris.

Function: In addition to depressing the foot it has a slight flexor action on the fore-arm, especially when the limb is well extended.

M. flexor antibrachii ulnaris (m.f.a.c.u.). Eisler (1895); Ribbing (1907).

Epitrochlo-cubital	Dugès (1834).
Flexor carpi	Stannius (1854-6).
Ulnaris	Mivart (1869).
Humero-ulnaris volaris	Hoffmann (1873-8).
Abaisseur du cubitus (38)	Perrin (1899).

Together with preceding muscle =

Flexor carpi ulnaris . Carus (1828); Rymer Jones (1852); Humphry (1872); Osawa (1902).

The second portion of the ulnar flexor muscle lies deep to the former. It is much smaller and forms a triangular block of muscle extending from its origin on the *epicondylus medialis humeri* to the proximal half of the ulna. It has a fleshy insertion on the outer edge of this bone.

Innervation: Like the former slip it is innervated by the N. ulnaris.

Function: The contraction of the muscle draws the fore-arm backwards—relative to the body—so that if the foot is resting on the ground it assists in advancing the body (cf. Perrin).

The following three muscles are accessory to the *M. flexor primordialis communis*. They are inserted on the dorsal side of its palmar tendon.

M. flexor accessorius lateralis (m.f.a.l.). Ribbing (1907).

Palmaris profundus III . . . Eisler (1895); McMurrich (1903).

Caput ulnare m. flex. dig. long. sublimis . . . Osawa (1902).

(For other homologies see *M. flex. prim. comm.*)

The *M. flexor accessorius* is a small muscle arising from the distal end of the ulna, from the ulnare+intermedium, and from basale 4. It passes obliquely radialwards and is inserted, as already stated, on the dorsal side of the palmar tendon of the *M. flex. prim. comm.*

Innervation: By N. ulnaris.

Function: It acts as an accessory flexor of the hand.

M. flexor accessorius medialis (m.f.a.m.). Ribbing (1907).

Palmaris profundus II . . . Eisler (1895); McMurrich (1903).

Caput ulno-carpale dig. long. sublimis . . . Osawa (1902).

With *M. pronator profundus* =

Pronator manus . . . Humphry (1872).

(For other homologies see *M. flex. prim. comm.*)

This muscle arises from the mesial side of the distal third of the ulna, from the mesial side of the ulnare+intermedium, and from the ulnar carpal. It runs parallel with the former muscle and is separated from it by the M. caput longum musculorum contrahentium (see below). Its insertion is likewise on the palmar tendon, anterior to the M. flex. acc. lat., and extending a little more proximally than does that muscle.

So far as Salamandra itself is concerned it seems a little pedantic to separate this muscle from the M. pronator profundus, and thus Humphry's term, Pronator manus, applied to the combined muscle, would appear to be the better term to use. Ribbing's arrangement has been adhered to, however, since his judgement is based on the study of an extensive series. It is impossible, nevertheless, to draw a sharp distinction between the two muscles.

Innervation: From N. ulnaris, R. medialis.

Function: As the former muscle.

MM. flexores breves superficiales (m.f.b.s.). Eisler (1895); McMurrich (1903); Ribbing (1907).

Flexor breves Carus (1828).

Flexores digitorum sublimes breves Osawa (1902).

(For other homologies see M. flex. prim. comm.)

These are small weak muscles which are really auxiliary to the M. flexor prim. comm., and are grouped with it by most authors. They arise from the dorsal surface of its palmar tendon, and from the edges of its digital tendons. They are inserted on the edges of the metacarpals, at the bases of the proximal phalanges, and, in the third finger, on the above mentioned (p. 85) auxiliary tendon which passes to the second phalanx.

M. caput longum musculorum contrahentium (m.c.l.c.). Ribbing (1907).

Flexor metacarpi IV profundus longus Eisler (1895).

Flexor profundus longus Osawa (1902).

Ulna-carpalis McMurrich (1903).

Together with MM. contrahentes digitorum =

Kurzer beuger Meckel (1828).

Flexor profundus digitorum Rüdinger (1868); Humphry (1872).

Flexor brevis Mivart (1869).

Ulnari-phalangei volares II-V Hoffmann (1873-8).

Fléchisseur accessoire des doigts (30 and 34) Perrin (1899).

This is a long slip of muscle arising from the mesial border of the proximal end of the ulna. It is inserted, by means of a fan-shaped tendon, on the several carpalia. It lies deep to the M. flex. prim.

comm., and its distal end separates the M. flex. acc. lat. from the M. flex. acc. med. Since the MM. contrahentes digitorum (see below) arise partly from the tendon of insertion of this muscle, as well as from the carpalia, Ribbing concludes that they originally formed a single muscle, and that the connexion with the carpalia is secondary.

Innervation: From the R. medialis N. ulnaris.

Function: It is the deep flexor muscle of the wrist.

MM. contrahentes digitorum (m.c.d.). Ribbing (1907).

Flexor breves medii s. contrahentes digitorum

Eisler (1895); McMurrich (1903).

Flexores digitorum profundi breves Osawa (1902).

(See also M. cap. long. musc. contra. for other homologies.)

These form a series of small flexor muscles which lie deep to the MM. flex. breves super., and superficial to the MM. flex. brev. prof. They arise partly from the tendon of insertion of the M. cap. long. musc. contra., and partly from the carpalia as follows:

The 4th digit. From the tendon and from the fourth and third carpalia.

The 3rd digit. From the tendon and mainly from the third carpal, but a few fibres arise from the second carpal also.

The 2nd digit. From the tendon and from the combined first and second carpal.

The 1st digit. From the tendon and from the combined first and second carpal, *not* from the carpal of the prepollex (see also p. 42).

All are inserted on the proximal ends of the corresponding proximal phalanges. Ribbing's result in not being able to find any connexion between these muscles and the tendon of the M. flex. prim. comm., described by McMurrich, is confirmed. Ribbing regards the muscles as being derived from the M. cap long. musc. contra. (see above).

Innervation: From the palmar branches of the NN. ulnaris and interosseus.

Function: They serve both to flex the fingers and, to a less extent, to approximate them towards one another.

M. pronator profundus (m.p.p.). Ribbing (1907).

Flexor indicis digiti proprius Rüdinger (1868).

Ulnari-metacarpi volares II-III Hoffmann (1873-8).

Palmaris profundus I Eisler (1895); McMurrich (1903).

Rotateur direct de la main (61) Perrin (1899).

With *M. flexor accessorius medialis* =

Pronator manus Humphry (1872).

With *M. interosseus antebrachii* =

Pronator radii Osawa (1902).

The deep pronator muscle arises from nearly the whole of the mesial side of the ulna, from the ulnare+intermedium, from the centrale and the third (and sometimes the fourth) carpal. It converges towards the radial side of the hand, where it is inserted on the radiale, on the carpal of the pre-pollex, on the combined first and second carpal, and, by means of a tendon, on the bases of the first and second metacarpals.

Innervation: From the *N. interosseus* which passes dorsal to it.

Function: To rotate the hand so as to bring the first digit nearer to the ground—i.e. pronation.

M. interosseus antibrachii. Eisler (1895); Ribbing (1907).

Cubito-digital Dugès (1834).

Pronator quadratus Mivart (1869); McMurrich (1903).

Pronator radii quadratus Humphry (1872).

Radio-ulnaris Hoffmann (1873-8).

Interosseus de l'avant bras (62) Perrin (1899).

Pronator Sieglbauer (1904).

With the *M. pronator profundus* =

Pronator radii Osawa (1902).

This muscle is very closely associated with the foregoing and arises from almost the whole of the mesial surface of the ulna. It is inserted on the distal three-quarters of the mesial surface of the radial, the fibres passing obliquely across the interosseal space between the two bones of the fore-arm. It may be exposed from the ventral side by removing the *M. pronator profundus*.

Innervation: From the *N. interosseus* which crosses its dorsal surface.

Function: It forms an elastic ligament between the two bones of the fore-arm.

MM. flexores breves profundi (m.f.b.p.). Eisler (1895); McMurrich (1903); Ribbing (1907).

Carpo-metacarpales Humphry (1872); Hoffmann (1873-8); Osawa (1902).

Fléchisseurs des métacarpiens (49-52) Perrin (1899).

These are four short, deep, flexor muscles which may be seen by removing the *MM. contra. dig.* They are separated from these muscles by the palmar branches of the flexor nerves, and arise

from the distal angles of the carpalia, while the most posterior muscle arises also from the ulnare+intermedium. They are inserted on the respective metacarpalia. It is noteworthy that the M. flex. brev. prof. of the first digit arises from the combined first and second carpal and *not* from the carpal of the pre-pollex. It is a very slight, narrow muscle, much smaller than the others.

Innervation: From the palmar branches of the NN. ulnaris and interosseus.

Function: They are the flexors of the metacarpalia.

MM. flexores digitorum minimi. Ribbing (1907).

Metacarpo-phalangei Humphry (1872); Hoffmann (1873-8).

Fléchisseurs primitifs des phalanges (45-8) Perrin (1899).

Metacarpo-phalangeales Osawa (1902).

These are very slight, narrow muscles which arise from about the middle of the ventral side of the metacarpals of the second, third, and fourth fingers, and are inserted on the proximal ends of the proximal phalanges of the corresponding digits. There is no representative of this series of muscles in the first digit.

Innervation: From the palmar branches of the NN. ulnaris and interosseus.

Function: Flexors of the digits.

M. interphalangeus digiti III (m.i.ph.3) (mihi).

Phalangeus Humphry (1872).

Interphalangeus digiti IV Hoffmann (1873-8); Eisler (1895); Ribbing (1907).

Fléchisseur primitif de la troisième phalangine (43) Perrin (1899).

Interphalangealis Osawa (1902); McMurrich (1903).

A very small, weak muscle arising from the ventral surface of the proximal phalanx of the third finger. It is inserted on the proximal end of the second phalanx of the same finger.

Innervation: From the N. interosseus.

Function: Flexor of the third digit.

MM. intermetacarpales (m.i.mc.). McMurrich (1903).

Interossei dorsales Rüdinger (1868).

Interossei Humphry (1872); Hoffmann (1873-8); Eisler (1895);
Osawa (1902); Ribbing (1907).

Intermétacarpiciens (53-5) Perrin (1899).

These are short triangular muscles lying between the digits connecting each finger with its neighbour. They can be fully seen from the ventral side only after removing the MM. flex. brev. prof.

They are attached to the metacarpals, and, although it is difficult to distinguish between 'origin' and 'insertion', nevertheless, since they occupy rather less of the *radial* side of a given metacarpal, they may perhaps be correctly regarded as arising from this side, and as being inserted on the whole of the *ulnar* side of the metacarpal of the adjoining digit.

Innervation: From NN. ulnaris and interossei.

Function: They are the adductors of the fingers, and serve to draw the digits towards one another.

MUSCLES OF THE TRUNK AND TAIL

(Pl. XVI, fig. 63 and Pl. XIX, fig. 71)

1. Historical.

The muscles of the trunk and tail regions have not been the recipients of much attention; in fact it is only necessary to cite two authors in order to cover the special literature relevant to the subject. The first of these is Maurer (1892), who made a careful study of the *ventral* body muscles of Urodeles and compared them with the corresponding muscles of fish. His work is quite well known. The *dorsal* trunk muscles of Urodeles have been investigated by Nishi (1916), who deals with *Cryptobranchus* and *Necturus*. The contributions of other workers are incidental rather than specific additions to our knowledge of these muscles.

2. Dorsal Trunk Muscles.

The dorsal body musculature remains very primitive and fish-like, and by most authors is treated generally as the dorsal muscle mass extending from the head to the tip of the tail. Nishi, however, distinguishes three portions.

M. dorsalis trunci (m.d.tr.). Nishi (1916).

Lateralis magnus (5)	Carus (1828).
Gemeinschaftlicher Rückgrats- und Kopfstrecker	Meckel (1828).
Dorsal muscle mass	Most authors.

The muscle forms the bulk of the dorsal muscle mass. It is completely segmented, being interrupted at each vertebra by a *myoseptum* which is attached to the neural spine and transverse processes of the vertebra. The myoseptum is not directly transverse but has a strong convexity caudalwards. Its edge is attached mesially to the strong connective tissue surrounding the median dorsal venom glands. Dorso-laterally it is attached to the skin. The dorsal edge of

the septum, that is, the free edge after the skin and glands have been removed, follows a peculiar course (see fig. 78). Commencing from the neural spine, at the caudal end of the vertebra, it passes very obliquely anterodorsally, and slightly laterally, to the level of the articulation with the vertebra next in front, where it reaches a point on the dorsal surface of the muscle immediately lateral to the median dorsal venom glands. It now turns sharply backwards at a very acute angle and passes in a postero-lateral direction to some distance behind the transverse process of the vertebra to which it belongs, and then curves round again so as to lie directly along the rib. It is continuous with the *inscriptio tendinea* of the ventral musculature.

The fibres of the *M. dorsalis trunci* run between the successive myosepta in an approximately sagittal direction. The whole muscle is very solid and powerful. In transverse section it is 'comma' shaped.

A fairly well-defined differentiation of this muscle mass is discernible on the dorsal side of the vertebrae, where a number of fibres arise from the postero-dorsal edge of the post-zygapophysis of one vertebra and are inserted along the dorsal surface of the neural arch of the vertebra next behind, thus filling the concavity which exists in this region on either side of the neural spine. This portion may be distinguished as the *M. interspinalis* (Nishi) (m.i.s.) (figs. 71 and 78), while that portion of the *M. dorsalis trunci* which passes between the transverse processes of the vertebrae may be distinguished by the name *M. intertransversarius*. This latter portion is distinguishable from the main mass only by the fact that it arises from, and is inserted on, the bone instead of the myoseptum.

The other region where some differentiation occurs is at the head. The condition is not essentially different from that in the body region, as described above, but the several portions are more easily distinguishable. Arising from the dorsal side of the transverse processes of the second and third vertebrae a strong muscle mass spreads out laterally, and is inserted over the postero-lateral aspect of the ear capsule. It extends anteriorly to immediately behind the dorsal end of the squamosal, and lies lateral to the superficial portion of the *M. lev. mandib. ant.* It is the *M. intertransversarius capitis superior* (Gaupp, in the Frog), or *M. longissimus capitis* (Nishi). As in *Necturus* it is traversed by three myosepta.

The *M. rectus capitis posterior* (Nishi), or *M. occipitalis* (Funk), is the mesial section of the spino-occipital musculature. It lies deep to the foregoing and to the *M. lev. mandib. ant.*, and arises from the neural spine and neural arch of the first vertebra. It spreads over the dorsal surface of the occipital region of the skull on to which it

is inserted. It is quite distinct from the *M. intertransversarius capitis superior*.

The *M. intertransversarius capitis inferior* (Gaupp, in the Frog) is really the direct continuation of the subvertebral musculature and arises from the transverse process of the second vertebra. It is inserted over the ventral surface of the occipital region of the skull, and is separated from the superior portion of the *intertransversarius* muscle by the first spinal nerve, and is necessarily antagonistic to it.

Innervation: In general the dorsal trunk muscles are innervated from the dorsal rami of the spinal nerves.

Function: Their general function is to produce a lateral flexion of the spine by alternate contraction on either side. The portions of the muscle attached to the skull similarly turn the head from side to side.

3. Ventral Trunk Muscles.

The muscles on the ventral side of the *sulcus lateralis* comprise two distinct series, the one—the *rectus* group—with fibres running parallel with the body axis, and the other—the *oblique* muscles—whose fibres are at an angle with this direction.

It is not easy to give synonyms for these muscles, since there is some variation among the different genera of Urodeles in which they have been investigated. The reader should, therefore, refer to Maurer's paper for a detailed comparison, but the following may be quoted as applying to *Salamandra*.

Funk (1827) calls the whole rectus muscle, including the *M. rectus cervicis*, the *M. hyoideo-ypsiloides*. Carus (1828) distinguishes the superficial from the deep portion and calls the former *abdominis musculus rectus* (8), and the latter *M. epischio-hyoideus* (7). He does not distinguish the 'cervical' from the 'abdominal' portions. Rymer Jones (1852) refers to the superficial portion as the *Rectus abdominis* and to the profundus portion as the *M. pubo-hyoideus*. He also does not separate the *rectus cervicis* and *rectus abdominis* muscles. Owen (1866) also calls the deep portion the *M. pubo-hyoideus*, while Hoffmann (1873-8) describes a muscle as the *M. pubo-thoracicus* (*Rectus abdominis*) which appears to represent the superficial portion of the muscle only, the profundus portion being undescribed. Hoffmann further distinguishes the *M. ypsiloides posterior* as the *M. pyramidalis*.

M. rectus abdominis superficialis (m.r.ab'). Maurer (1892).

This portion of the rectus muscle forms a large flat sheet covering the ventral parietes of the abdomen, the right and left halves being

separated by a wide median aponeurosis, or *linea alba*. The muscle may be regarded as extending from the anterior edge of the pubis to the level of the sternal cartilage, and is interrupted by ten *inscriptiones tendineae*—not counting the terminal inscription lateral to the sternum. It is, therefore, difficult to speak of 'origin' and 'insertion', since each inscription is firmly attached to the overlying skin. The direction of the fibres is longitudinal. The muscle is fairly easily separable into two portions, namely, a thicker mesial and a thinner lateral section, while the epigastric arteries run along the line of junction between them. Anteriorly the fibres take several courses, the most lateral merge into the *M. pectoralis*, the most mesial fibres pass dorsal to this muscle and are inserted on the postero-lateral edge of the sternal plate, and on the pericardium, while the remainder of the muscle continues directly forwards, dorsal to the coracoids, as the *M. rectus cervicis superficialis* (q.v.), and is inserted on the hyo-branchial apparatus. In addition to its attachment to the pubis a few of the posterior fibres are inserted on the lateral processes of the ypsiloid cartilage.

M. rectus abdominis profundus (m.r.ab."). Maurer (1892).

This muscle also extends from the pelvis to the hyoid, but unlike the superficial portion it lies more or less free throughout nearly its whole length. It arises from the anterior edge of the pubes deep to the superficial stratum, and is also interrupted by tendinous inscriptions of which only one or two of the most caudal are attached to those of the *M. rect. abd. super.*, the remainder being entirely free. Anteriorly the muscle becomes rather more lateral in position and the inscriptions fail to correspond exactly with those of the other muscles, and also tend to become less distinct. This is doubtless to be explained by supposing that the freedom of the muscle has allowed a certain amount of stretching of the myomeres to occur.

The portion of the muscle anterior to the sternum forms the *M. rectus cervicis profundus* (q.v.)

Innervation: Both sections are innervated by the terminal branches of the spinal nerves 5–15 inclusive.

Function: In general they serve to flex the vertebral column, while they also act on the hyo-branchial apparatus and tend to compress the viscera.

M. ypsiloides anterior. Whipple (1906).

Consisting of only a few fibres which take their origin from the anterior edge of the lateral processes of the *ypsiloid cartilage*, and

which have their insertion in the inscription next anterior, this muscle is scarcely to be distinguished from the remainder of the M. rectus abdominis superficialis, from which it is derived.

Innervation: By the terminal branches of N. spinalis 14.

Function: It is the elevator of the *cartilago ypsiloidea*.

M. ypsiloideus posterior (m.y.p.). Whipple (1906).

M. pyramidalis Most other authors.

This is a larger, more powerful, and better defined muscle, although its derivation from the rectus abdominis is still apparent. It arises from the antero-dorsal edge of the pubis deep to the M. rect. abd. prof. and spreads in a more or less fan-like manner to be inserted on the ypsiloid cartilage—on the lateral edges of the shaft, and the posterior edges of the lateral processes. The muscle is thicker at its lateral edges than mesially, and has considerable power.

Innervation: By twigs from the combined nerve formed from NN. spinales 14 and 15 (? N. ileo-hypogastricus).

Function: It is the depressor of the ypsiloid cartilage (see also p. 45).

The *M. obliquus externus* forms the most superficial layer of the lateral body-wall muscles. Like the rectus muscle it is divisible into superficial and deep strata. With regard to synonyms, Funk (1827) refers to the muscles of the lateral body-wall collectively as MM. intercostales, and while later authors dealing with the body muscles of Urodeles (mainly Cryptobranchus), e.g. Humphry, Mivart, Hoffmann, &c., make some distinction between the several layers, their views are not always identical, and there is also considerable variation in the relative development of the various strata in different genera. It is therefore better that the reader should refer to Maurer's paper for a comparative discussion, than to attempt to correlate these authors' synonyms here.

M. obliquus externus superficialis (m.o.s.). Maurer (1892).

The fibres of this portion arise dorsally from the ribs immediately ventral to the *sulcus lateralis*, and also from the several *inscriptiones tendineae* which are continuous with their lateral extremities. The insertion is mainly on the ensuing inscription, but the most ventral fibres terminate along a line joining the shoulder-joint with the hip, and are inserted into a tendinous sheet which passes over the rectus muscles, ventrally, to the opposite side. This tendon, as well as the intermuscular inscription, is closely applied to the skin, and is very difficult to separate therefrom. The muscle extends from the rib of

the third vertebra to the sacrum. The fibres run in an oblique direction from antero-dorsal to postero-ventral.

M. obliquus externus profundus. Maurer (1892).

The deep stratum is an even thinner sheet of muscle than that just described. To expose this layer it is better to commence removing the superficial stratum from the ventral edge, as it is more easily separable there than at the dorsal edge. It is entirely similar to the superficial layer in origin and insertion, but the direction of its fibres tends to become more longitudinal.

Innervation: Both parts are innervated from the ventral rami of NN. spinales 5-15.

Function: In general both layers serve to contract the body wall and consequently to compress the body cavity, but the specific results of its action vary according to whether it is antagonistic or complementary to its neighbouring muscles.

The *most internal layer* of the ventral trunk muscles is, according to Maurer, composed of three parts which, in higher forms, separate into distinct muscles, but which, in *Salamandra*, are not clearly separable one from another.

The most dorsal and mesial section, lying next to the vertebral column, is the *pars subvertebralis* (m.s.). It passes from vertebra to vertebra and is attached to the lateral part of each centrum and to the ventral face of each transverse process. Its lateral edge may be roughly defined as the point at which the spinal nerves emerge, but apart from the separation thus caused it merges quite imperceptibly into the *pars transversalis*.

The *pars transversalis* is similarly attached to the ventral surfaces of the ribs, and, at their lateral extremities, merges in turn into the *pars obliqua interna*.

The *pars obliqua interna* is attached to the myosepta which are continuous with the ribs.

The direction of the fibres of the several portions varies. The subvertebral portion is longitudinal; the *pars transversalis* becomes rather more oblique, while the *pars obliqua interna* is very markedly so. The fibres of this latter portion pass from antero-ventral to postero-dorsal and cross those of the *M. obliquus externus* almost at a right angle. The *pars obliqua interna* extends from the shoulder to the pelvis. The anterior fibres are inserted around the bases of the lungs and on the pericardium and help to form the diaphragm (see also p. 270). The other two portions are virtually

continuous from the head to the tip of the tail, although the subvertebral portion is somewhat deficient in the sacral region. The anterior fibres are inserted on the postero-ventral aspect of the occipital region of the skull.

Innervation: From the ventral rami of the spinal nerves.

Function: The *pars subvertebralis* flexes the spine. The *pars transversalis* also tends to flex the spine if both sides contract simultaneously, but if they contract alternately then a lateral flexion of the spine would occur. The function of the *pars obliqua interna* is similar to that of the *obliqua externa* (q.v.).

4. Caudal Muscles.

The *caudal muscle mass* is dorsally very similar to that of the body. The anterior part forms the *M. ilio-caudalis* (m.il.cd.), the fibres of which arise from the first two or three caudal vertebrae and are inserted on the ilium. The dorsal and ventral muscles of the tail are continuous laterally, forming strong C-shaped masses of muscle on either side of the vertebrae. In the mid-ventral line the muscles of the two sides are separated by a tough ligament which attaches the spines of the haemapophyses to the skin, while dorsally there is a deep median groove between the muscles wherein lie the cutaneous glands.

The ventral muscle of the tail shows some slight tendency to differentiation in so far as some of the fibres pass from one haemapophysis to the next instead of lying between myosepta, but the distinction is not clear enough to justify their separation as an individual muscle.

Innervation: From both dorsal and ventral rami of the spinal nerves.

Function: They obviously serve as the motors of the tail.

MUSCLES OF THE HIND-LIMB AND PELVIS

(Pls. VIII and XVI)

1. Historical.

In general the hind-limb does not seem to have received so much attention as the fore-limb. One of the earliest workers to make a special study of its muscles is Perrin (1892). His work is very careful and detailed, but, as has already been noted in discussing his work on the arm muscles, it suffers from the absence of correlation with the nerves. Eisler's work (1895), already mentioned, covers

the hind-limb as well as the arm, as also does that of Sieglbaur (1904). McMurrich (1904) made a study of the phylogeny of the crural flexors and their nerves, and, while he does not deal expressly with *Salamandra*, his work is of sufficiently general nature to have a bearing on the problems involved. Most of his observations were made on serial sections, and this has caused him to draw one or two conclusions which scarcely seem justified when viewed in the light of actual dissections. These conclusions are criticized by Ribbing (1909) and will be referred to again later. Ribbing's work is very sound and has the advantage that the results are correlated with those obtained for the fore-limb. More recently a phylogenetic study of the muscles and nerves of the post-axial region of the tetrapod thigh has been undertaken by Appleton (1928), who describes the condition found in the Salamander, while Low (1926-9) has studied the development of the pelvic girdle and its muscles in a number of Urodeles (but not *Salamandra*) and throws some light on the phylogeny of certain muscles.

2. Muscles of the Pelvis and Thigh (Pl. VIII, figs. 48 and 49).

On removing the skin from the ventral surface of the pelvis and the base of the tail the following three muscles may be observed. They are grouped together by Appleton as the *Caput ventrale*, *M. flexor cruris*.

M. pubo-ischio-tibialis (m.p.i.t.). de Man (1873); Osawa (1902); Low (1926).

Rectus	Funk (1827).
Gracilis cruris flexor (35)	Carus (1828).
Zweiter Beuger	Meckel (1828).
Sous-ischio-tibial	Dugès (1834).
Flexores abducentes	Stannius (1854-6).
Depressor and Adductor of the pelvic limb	Owen (1866).
Gracilis	Mivart (1869).
Superficial stratum of Plantar muscles of Thigh (Gracilis + Semitendinosus + Semimembranosus)	Humphry (1872).
Pubo-ischio-tibialis (Semitendinosus)	Hoffmann (1873-8).
Fléchisseur du tibia (110-11)	Perrin (1892).
Rectus femoris	Eisler (1895).

This is the most superficial muscle of the pelvis as seen from the ventral side. It arises just lateral to the pubo-ischiadic symphysis and covers the *M. pubo-ischio-femoralis externus* with the exception of a narrow strip anteriorly. It passes right down the ventral surface of the thigh and is inserted on the tibia. It is wide and thin at its

origin and converges rapidly while passing under the pelvic girdle to form a narrower, thicker muscle which tapers only slightly while passing down the thigh. Anteriorly it has a tough fibrous connexion with the M. pubo-tibialis, while at its posterior border it receives the M. caudali-pubo-ischio-tibialis which is inserted into it by means of a tendon at about the level of the proximal end of the femur. This is an excellent example of the rare phenomenon of one muscle being inserted into another, the fibres of the two muscles being approximately at right angles.

Innervation: From the N. ischiadicus ventralis which passes between this muscle and the M. pub. isch. fem. ext. The fibres enter the muscle from the dorsal side.

Function: It either serves to flex the knee, or, if the extensor muscles are antagonistic, the flexion would occur at the hip and it would depress the foot towards the ground.

M. pubo-tibialis (m.p.t.). de Man (1873); Hoffmann (1873-8).

Vastus	Funk (1827).
Anticus cruris protractor (34)	Carus (1828).
Grösster Beuger	Meckel (1828).
Pubo-sous-tibial	Dugès (1834).
Gracilis	Stannius (1854-6).
Protractor or flexor of the thigh	Owen (1866).
Sartorius	Mivart (1869); Eisler (1895).
Gracilis part of the superficial stratum of the plantar muscles	

Humphry (1872).

Adducteur du tibia (106-8) Perrin (1892).

This muscle has a tendinous origin from the antero-ventral edge of the pelvic girdle, i.e. from the pubic cartilage, in front of the obturator foramen. It passes along the antero-ventral border of the thigh and is inserted on the anterior face of the proximal end of the tibia, close to the M. pub. isch. tib. It is a narrow muscle, more or less oval in cross-section, and of medium strength.

Innervation: From N. ischiadicus ventralis.

Function: It serves mainly to adduct the limb, i.e. to draw it towards the body, but it also has a slight flexor action on the knee-joint.

M. ischio-flexorius (m.is.f.). de Man (1873); Eisler (1895); Osawa (1902); Low (1926).

Plantae pedis (38)	Carus (1828).
Langer, starker Beuger	Meckel (1828).
Flexor of the leg	Rymer Jones (1852).

Flexores abducentes	Stannius (1854-6).
Semitendinosus	Mivart (1869).
Cau-do-pedalis	Humphry (1872).
Ischio-flexorius (Semimembranosus)	Hoffmann (1873-8).
Fléchisseur externe de la jambe (115)	Perrin (1892).
Proximal portion =	
Ischio-flexorius	McMurrich (1904).
Distal portion =	
Plantaris superficialis medialis	McMurrich (1904).

A strap-like muscle, which arises from the posterior ventro-lateral angle of the os ischium, immediately behind the M. pub. isch. tib. During its course along the ventro-posterior border of the thigh it passes dorsal to the insertion of the M. caud. pub. isch. tib. into the M. pub. isch. tib. At the popliteal region it becomes more mesial and passes to about the middle of the flexor surface of the leg, and, at a point about midway between the knee and the ankle, it disappears into a tendon which mingles with the plantar aponeurosis of the M. flexor primordialialis communis.

This muscle had always been regarded as a single muscle until 1904, when McMurrich, during his investigation of *Amblystoma*, noticed that its fibres were interrupted by a tendinous inscription at about the level of the knee, and hence he suggested that the muscle was really composed of two separate muscles fused end to end. The proximal portion he regarded as the true ischio-flexorius, but the distal portion he thought was the serial homologue of the superficial flexor muscle of the fore-arm, which arises from the humerus (M. flex. prim. comm.), and he named it accordingly M. plantaris superficialis medialis. McMurrich based his view largely upon the appearance of the cross-section of the leg just below the knee compared with that of the fore-arm below the elbow, and on the fact that otherwise a superficial flexor with *parallel longitudinal* fibres is wanting in the hind-limb (*vide infra*).

In *Salamandra* the relations of the M. ischio-flexorius are very similar to those described by McMurrich for *Amblystoma*. That two muscles are involved in the composition of this adult 'ischio-flexorius' seems almost certain, since the innervation of the two portions is different. While it may be that McMurrich's interpretation is correct it is nevertheless open to doubt, and, until a thorough investigation of the ontogeny of the muscle is available, it seems preferable to retain the name 'ischio-flexorius' for the whole muscle and to apply the term *pars propria* to the proximal portion, and *pars plantaris* to the distal portion.

Innervation: *Pars propria* is supplied from N. ischiadicus ventralis and *pars plantaris* from N. sciaticus.

Function: It is an auxiliary flexor of the knee-joint, and, by virtue of its insertion into the plantar aponeurosis, of the toes also.

M. caudali-pubo-ischio-tibialis (m.c.p.i.t.). de Man (1873); Hoffmann (1873-8); Low (1926).

Parvus cruris retractor (37) Carus (1828).

Subcaudalis Meckel (1828); Stannius (1854-6).

Coccy-sous-fémoral Dugès (1834).

A long muscular slip Rymer Jones (1852).

Semimembranosus Mivart (1869).

Caudo-crural Humphry (1872).

Déducteur caudal inférieur de la cuisse (112) . . . Perrin (1892).

Caudali-pubo-ischiadicus Osawa (1902).

Together with *M. caudali-femoralis* =

Caudofemoralis Appleton (1928).

This is the middle member of the three ventral caudal muscles which separate from the general subvertebral muscle mass of the tail at the level of the first haemal-arch (fourth caudal vertebra). They may in fact be regarded as arising from this bone, and from the transverse processes of the vertebra. The other two muscles of this series are the *M. ischio-caudalis*, on its mesial side, and the *M. caudali-femoralis* lateral to it. The unusual character of its insertion has already been mentioned, namely, by means of a flat tendon into the posterior edge of the *M. pub. isch. tib.* The direction of its fibres is almost at right angles to those of the latter muscle.

Innervation: From N. pudendus.

Function: Its main function must be to flex the tail. Whether it has any action on the limb is doubtful.

M. ischio-caudalis. Hoffmann (1873-8); Osawa (1902); Low (1926).

Caudae flexor (43) Carus (1828).

Flexor of the tail Rymer Jones (1852).

Ischio-caudal Mivart (1869); Humphry (1872).

Forming the most mesial of the three muscles arising from the fourth caudal vertebra, as above described, it passes directly forwards between the *M. caud. pub. isch. tib.* and the cloaca, and is inserted on the posterior border of the ischium. It is a flat, ribbon-like muscle, and, in the male, it passes between the dorsal and ventral portions of the cloacal gland.

Innervation: From N. pudendus.

Function: It is a flexor of the tail. Together with the former

muscle it must have a special function in the male by compressing the glandular tissue around the cloaca. It is probably for this reason that the tail is strongly flexed during copulation.

M. caudali-femoralis (m.cd.fm.). de Man (1873).

Tricipitum, capita media	Funk (1827).
Longus femoris reductor et attractor (32)	Carus (1828).
Pyriformis	Meckel (1828); Stannius (1854-6).
Coccy-sus-fémoral	Dugès (1834).
Long extensor and Adductor of the thigh	Rymer Jones (1852).
Femoro-caudal	Mivart (1869).
Caudo-femoralis	Humphry (1872); Osawa (1902); Low (1926).
Caudali-femoralis (pyriformis)	Hoffmann (1873-8).
Déducteur caudal supérieur de la cuisse (116)	Perrin (1892).

Together with Caudali-pubo-ischio-tibialis =

Caudo-femoralis	Appleton (1928).
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Like the other two muscles, already described, which arise from the fourth and fifth caudal vertebrae, it is a narrow, strap-like muscle with an oval cross-section. It is the most powerful muscle of the three, and the most lateral. At what Appleton terms 'the posterior groin' it turns lateralwards to enter the leg just dorsal to the *M. ischio-flexorius*. It is inserted on the femur, at about a third of its length from the pelvic girdle, on a slight tuberosity which may probably be regarded as the *external trochanter*.

Innervation: From the *N. pudendus*.

Function: It serves either to flex the tail in a lateral direction or to retract the femur, according to circumstances.

The deeper flexors are two in number, and are exposed to view on removing the *MM. pubo-ischio-tibialis* and *caudali-pubo-ischio-tibialis*.

M. pubo-ischio-femoralis externus (m.p.i.f.e.). de Man (1873); Osawa (1902); Low (1926).

(?) <i>Cruraeus anticus</i>	Funk (1827).
<i>Crassus cruris flexor</i> s. <i>attractor et reflexor</i> (36)	Carus (1828).
<i>Nach aussen Zieher</i>	Meckel (1828).
<i>Ex-pelvi-fémoral</i>	Dugès (1834).
<i>Obturatorius et adductor ischiadicus</i>	Stannius (1854-6).
<i>Adductor</i>	Mivart (1869).
Middle part of deeper stratum (adductors and external obturator)	
	Humphry (1872).
<i>Pubo-ischio-femoralis-externus</i> (pectineus)	Hoffmann (1873-8).
<i>Fléchisseur du fémur</i> (119)	Perrin (1892).
<i>Obturator anterior and posterior</i>	Appleton (1928).

This muscle arises from the ventral surface of the pelvic girdle, its posterior portion lying deep to the M. pub. isch. tib. It tapers sharply, so that it has a triangular shape when seen from the ventral side. It is inserted along the middle of the ventral surface of the femur. Appleton regards the muscle as being composed of two sections, and calls them respectively obturator anterior and posterior. There is considerable justification for this view, but, since in the adult they have fused indistinguishably into a single mass, the older name is adhered to. There is, however, an anterior slip of muscle arising from the pubis which is distinct, but which was probably included by the older authors as forming part of the muscle just described (see p. 106).

Innervation: This muscle has a double innervation in accord with its double nature. The anterior fibres (Appleton's obturator anterior) are supplied by the obturator nerve, while the posterior fibres (Appleton's obturator posterior) receive their supply from the N. ischiadicus ventralis.

Function: It is the true flexor of the hip-joint.

M. ischio-femoralis (m.is.fm.). Mivart (1869); de Man (1873); Osawa (1902).

Gemellus	Meckel (1828).
„ s. quadratus femoris	Stannius (1854).
Anterior abductor	Rymer Jones (1852).
Hinder (ischio-femoral) part of deeper stratum of thigh								Humphry (1872)
Ischio-femoralis (quadratus femoris)	Hoffmann (1873-8).
Rotateur inverse du fémur (124)	Perrin (1892).
Ischio-femoralis α and β	Low (1926).

Together with previous muscle =

Flexor profundus Appleton (1928).

This is a small, short muscle which arises from the posterior sector of the concave lateral border of the ischium, and passes in a latero-dorsal direction to its insertion on the posterior face of the head of the femur.

Innervation: From N. ischiadicus ventralis.

Function: It tends both to depress and to retract the femur, or, conversely, to support and project the pelvis.

With reference to the phylogeny of the ventral thigh muscles described above, the conclusions of Appleton (1928, p. 427) may be quoted.

‘It is concluded that some modification has occurred in the superficial ventral thigh muscles of Urodela to which the extensive distribution of N. ischiadicus

ventralis may be attributed. In them again, there is a rectus internus (Humphry). There is no reason to believe that either this or the pubotibialis (with metazonal innervation) were ever present in pro-Reptilia. A study of modern Urodela, moreover, points to a progressive differentiation of *M. pubotibialis*, with the formation of an "adducteur du fémur" (Perrin) perhaps better distinguished as a distinctive urodele formation by the term *M. pubifemoralis*. . . . The femoro-fibular muscle (Humphry) of urodeles appears to be a caenotelic structure, being apparently unrepresented in Salientia and Amniota. There is, again, no definite evidence that the fore-runners of Amniota ever possessed the caudocrural muscle (of Humphry), which has probably been derived in urodela from a common caudofemoral mass along with the caudalifemoralis (of de Man).

'The attachments of the caudo-crural and the course of the N. perinealis favour this interpretation rather than a derivation of the caudocrural from the ischiocaudal.'

M. pubo-ischio-femoralis internus (m.p.i.f.i.).¹ de Man (1873); Sieglbauer (1904); Low (1926).

Crassus femoris tensor s. protractor (31) Carus (1828).

Pectineus Meckel (1828); Stannius (1854-6); Appleton (1928).

Intra-pelvi-fémoral Dugès (1834).

Iliacus Mivart (1869).

Anterior-suprapubic-portion of the deeper stratum of the plantar of thigh s. pectineus Humphry (1872).

Pubo-ischio-femoralis internus (Adductor) Hoffmann (1873-8).

Extenseur du fémur (121)² Perrin (1892).

Together with *M. extensor iliotibialis* =

Extensor femoris biceps (Caput pubicum) Osawa (1902).

A very large, powerful muscle arising from the whole internal face of the pubis, and from part of that of the ischium and ilium. It bends around the anterior edge of the pubis, and passes down the anterior aspect of the thigh. It is inserted along the whole anterior face of the femur with the exception of the extreme ends. As disclosed by its innervation it belongs to the dorsal, or extensor muscles.

Innervation: From N. femoralis, and a few twigs proximally from N. obturatorius.

Function: It has only a relatively slight influence in extending the limb in a dorso-ventral plane, but has a very pronounced action in drawing the femur towards the body anteriorly.

CRITICISM OF PERRIN.

Hoffmann describes a muscle under the name 'Pubo-ischio-femoralis internus' which he says 'von der oberen (Bauch-) Fläche

¹ See also *M. pubo-extensorius*, p. 106.

² See 'Criticism of Perrin'.

des *Os pubo-ischii* entspringt', while Perrin (1892) in describing what he claims to be the homologous muscle (viz. his Adducteur du fémur, 117) says: 'Son aponéurose d'insertion occupe à la face ventral du pubis, le bord antérieur depuis l'épine pubienne jusqu'au commencement du dernier tiers.' His figures confirm this origin from the *ventral* face of the *pubis* only. The same author, later on, describes and figures two muscles (Déducteur du fémur, 120, and Extenseur du fémur, 121) which he considers to be the homologues of the ileo-femoralis of Hoffmann. Of the latter muscle he says: 'C'est un muscle puissant dont l'insertion supérieure est tout entière sur la face dorsale du bassin où elle recouvre tout le pubis, l'angle antéro-interne de l'ischion, et l'extrémité antérieure de l'ilion.'

Both his descriptions and his figures of these two muscles correspond exactly with Hoffmann's ilio-femoralis and pubo-ischio-femoralis internus respectively. Perrin himself seems to be aware of some discrepancy, since he remarks at the conclusion of his description of the *extenseur du fémur* that 'Hoffmann les fait sortir uniquement de l'ilion . . .'

The muscle which Perrin homologizes with Hoffmann's pubo-ischio-femoralis internus (his Adducteur du fémur) is most probably included by Hoffmann, and the other authors, in the muscle Hoffmann calls M. pubo-ischio-femoralis externus. The validity of this arrangement is questionable since the innervation is different from that of the adjoining part of the M. pub. isch. fem. ext. Following Appleton's suggestion it is therefore described here as a separate muscle, M. pubi-femoralis.

M. pubi-femoralis (m.p.fm.). Appleton (1928).

Adducteur du fémur (117) Perrin (1892).

This muscle arises from the antero-ventral surface of the pubo-ischium, immediately anterior to the M. pub. isch. fem. ext., and deep to the M. pub. tib. Some fibres arise from a common raphe with this latter muscle. It is relatively weak, and passes obliquely lateralwards to be inserted along the ventral face of the femur, antero-distally from the M. pub. isch. fem. ext. and posterior to M. pub. isch. fem. int.

Innervation: From N. ischiadicus ventralis.

Function: It serves to draw the femur towards the body anteriorly.

M. pubo-extensorius. Low (1926).

This muscle is only described by Low. By other authors it is included in the M. pub. isch. fem. int., with which muscle it is very

closely associated in the adult (although from his figure it would appear to correspond with Humphry's *rectus femoris*), nevertheless it has an insertion distinct from this muscle and is fairly easily separable from it, so that, in view of the fact that Low finds it more distinct in the larva (he has not investigated *Salamandra*), it seems justifiable to include it as a separate muscle.

In *Salamandra* the muscle takes its origin from the antero-dorsal edge of the pubis and passes lateralwards along the antero-dorsal aspect of the thigh to a tendinous insertion on the knee capsule. Although very closely associated with the M. pub. isch. fem. internus, it is distinguishable from this muscle distally by its insertion, and, starting from this end, it may be fairly easily peeled away from it proximally.

Innervation: From N. femoralis.

Function: It is an extensor of the thigh.

The remaining three thigh muscles are quite superficial and are strictly dorsal in position (Pl. VIII, fig. 47).

M. extensor iliobtibialis (m.e.il.t.). Appleton (1928).

Cruraeus posticus	Funk (1827).
Longus cruris abductor (33)	Carus (1828).
Starker Strecker	Meckel (1828).
Long abductor of the leg	Rymer Jones (1852).
Streckmuskelmasse des Unterschenkels	Stannius (1854-6).
Retractors or extensors of the thigh and leg	Owen (1866).
Glutaeus maximus. Rectus femoris	Mivart (1869).
Middle sector of the Ilio-crural s. gluteo-rectus	Humphry (1872).
Ilio-tibialis	de Man (1873).
Ileo-extensorius (extensor cruris)	Hoffmann (1873-8).
Extenseur superficielle du tibia; Tête externe inférieur, et Tête externe supérieur	Perrin (1892).
Rectus femoris	Eisler (1895).
Ileo-extensorius	Sieglbauer (1904); Low (1926).

Together with M. pubo-ischio-femoralis internus =

Extensor femoris biceps (Caput iliacum) Osawa (1902).

This muscle arises by two separate heads from the dorso-lateral surface of the ilium and passes superficially along the dorsal, or extensor, surface of the thigh to the knee. The two heads usually unite, more or less, for a short distance proximal to the knee, although they may remain separate and appear as two discrete muscles. In either case their distal ends pass into a strong flat tendon which fuses with the connective tissue of the knee capsule, and finally attaches itself to the

tibial spine, passing between the MM. extensor digitorum communis and extensor cruris tibialis in order to do so. Both sections are narrow, oval in cross-section, and of medium strength.

Authors have homologized this muscle in different ways. Humphry and Mivart, in *Cryptobranchus*, and Noble in the *Salientia*, regard it as composed of two distinct muscles. De Man, in *Triton*, regards any separation into two sections as artificial. Perrin, in *Salamandra*, describes it as one muscle with two heads, while Appleton—whose name is adopted here—in his list of muscle homologies (Part II, pp. 434-5) calls it *M. extensor iliotibialis*, and distinguishes the two heads as *pars anterior* and *pars posterior*, while the same author in another place (Part I, p. 378, fig. 2) labels the former section *Ilio-tibialis*, and the latter *Ilio-extensorius*, thus following Noble.

Innervation: From N. extensorius.

Function: True extensor of the leg.

M. ilio-fibularis (m.il.f.). de Man (1873); Sieglbaur (1904); Osawa (1902); Appleton (1928).

Semimembranosus	Funk (1827).
Wadenbeinbeuger	Meckel (1828).
Ileo-peronien	Dugès (1834).
Abductor fibularis primus	Stannius (1854-6).
Ileo-peroneal	Mivart (1869).
Biceps flexor cruris (outer or ilio-fibular sector)	Humphry (1872).
Déducteur du fibula (113)	Perrin (1892).
Ilio-femoro-fibularis	Low (1926).

Together with *M. femoro-fibularis* =

Ileo-femoro-fibularis (biceps) Hoffmann (1873-8).

Most authors regard this muscle as the long head of a biceps femoris muscle. The validity of this is doubtful, and the question will be discussed in detail after the description of what is regarded by these authors as the short head, namely, the *M. femoro-fibularis*.

The *M. ilio-fibularis* arises from the external face of the ilium, posterior to the *M. extensor ilio-tibialis*. It passes down the posterodorsal border of the thigh to its tendinous insertion on the proximal end of the fibula. The N. peroneus passes over its *dorsal* edge at its insertion. It is a relatively weak muscle.

Innervation: From N. extensorius.

Function: In conjunction with the *M. extensor ilio-tibialis* it would tend to *extend* the leg, but acting with the *M. pubo-tibialis*

it would tend to *flex* it. Probably the latter is its principal and stronger function.

M. femoro-fibularis (m.fm.f.). Humphry (1872); Osawa (1902).

Popliteal	Carus (1828).
Fémoro-péronien	Dugès (1834).
Abductor fibularis secundus	Stannius (1854-6).
Fléchisseur primitif du fibula (114)	Perrin (1892).
Ilio-femoro-fibularis	Low (1926).

Together with *M. ilio-fibularis* =

Ileo-femoro-fibularis (biceps)	Hoffmann (1873-8).
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This muscle is considered here on account of its supposed association with the preceding one, although it hardly belongs to the thigh muscles proper. It is a short, narrow muscle band arising from the median ventral face of the femur, near the distal end, and, passing across the popliteal space behind the knee, is inserted on the posterolateral face of the proximal end of the fibula.

Innervation: From N. sciaticus.

Function: It is the direct flexor of the knee.

This muscle is regarded by Hoffmann and most of the earlier authors as the short head of a biceps muscle, of which the other longer head is the *M. ilio-fibularis*. Hoffmann states that the two muscles are joined at their insertion, but this is incorrect so far as *Salamandra* is concerned, for, although their insertions are always close together, they are easily and naturally separable. The strongest fact against regarding the two muscles as the two heads of a biceps is that their innervation is entirely different, the *M. ilio-fibularis* being innervated by the dorsal nerve—N. extensorius—and the *M. femoro-fibularis* by the ventral, or flexor nerve—N. sciaticus. It therefore seems more correct to regard them as two distinct and unrelated muscles, and this is the view held by the later writers, e.g. Perrin and Appleton. The latter author regards the *M. femoro-fibularis* as 'a caenotelic structure, being apparently unrepresented in *Salientia* and *Amniota*' (see also p. 105).

M. ilio-femoralis. de Man (1873); Osawa (1902); Low (1926); Appleton (1928).

Ileo-rotulien	Dugès (1834).
Thick flexor of the thigh	Rymer Jones (1852).
Gluteus	Stannius (1854-6).
Gluteus medius and minimus	Mivart (1869).
Ileo-femoral stratum of the dorsal muscles of the thigh	

Humphry (1872).

Ileo-femoralis (Iliacus)	Hoffmann (1873-8).
Déducteur du fémur (120) ¹	Perrin (1892).

This is the deepest of the dorsal thigh muscles. It takes its origin from the postero-lateral face of the ilium, and to some extent from the dorsal (inner) face of the ischium also. It is inserted along the middle portion of the posterior face of the femur. Low (1926) distinguishes the anterior from the posterior portion.

Innervation: From N. extensorius.

Function: It tends to draw the femur towards the tail and is therefore the opposer of the M. pub. isch. fem. int.

3. Extensor Muscles of the Leg and Foot (Pl. VIII, fig. 47).

These should be dissected from the dorsal side.

M. extensor digitorum communis (m.e.d.). Funk (1827); Ribbing (1909).

Longus digitorum extensor (40)	Carus (1828).
Péronéo-sus-digital.	Dugès (1834).
Extensor longus digitorum pedis	Rymer Jones (1852).
Extensor hallucis longus, et Extensor quatuor digitorum longus	Schmidt, Goddard, and van d. Hoeven (1864).
Extensor longus digitorum	Mivart (1869); Humphry (1872).
Femoro-digiti I-V	Hoffmann (1873-8).
Extenseur des metatarsiens	Perrin (1892 a).
Extenseur commun des doigts (76)	Perrin (1892).
Extensor digitorum longus	Osawa (1902).
Femoro-metatarsalis	Sieglbaur (1904).

Together with the following muscle =

Extensor digitorum communis longus	Eisler (1895).
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This is the most superficial muscle on the extensor side of the leg. It arises from the *epicondylus lateralis femoris*, between the MM. extensor cruris tibialis and fibularis, by means of a narrow tendon. The muscle spreads out rapidly and becomes thin and fan-shaped. At the bases of the digits it breaks up into nine small tendons, eight of which are inserted on either side of the bases of the metatarsals of the four post-axial digits, while the remaining one is inserted on the fibular side of the first metatarsal. Sieglbaur denies the existence of this ninth tendon, but it certainly exists in the majority of cases, if not in all. There is a slight aponeurosis between the proximal portion of this muscle and the M. extensor cruris fibularis.

Innervation: By the NN. dorsales pedis, from N. peroneus.

Function: It is the chief extensor of the foot.

¹ See also 'Criticism of Perrin', pp. 105-6.

M. extensor tarsi tibialis (m.e.t.t.). Ribbing (1909).

Rotateur inverse du pied (92)	Perrin (1892).
Extensor tarsi tibialis longus	Eisler (1895).

Together with *M. extensor cruris tibialis* =

Tibialis anticus	Funk (1827); Schmidt, Goddard, and van d. Hoeven (1864); Humphry (1872).
Abductor et flexor pedis + introflexor pedis (39).	Carus (1828).
Femoro-tibialis	Hoffmann (1873-8).
Tibialis	Osawa (1902); Sieglbaur (1904).

This is a small muscle which arises from the *epicondylus lateralis femoris* very close to, or from a common tendon with, the *M. ext. dig. comm.* Although its origin is slight, the fibres soon swell into a spindle-shaped muscle of moderate size which passes alongside the *M. extensor cruris tibialis* to be inserted on the ventral surface of the tibiale and cart. pre-hallucis. It is easily separated from the neighbouring muscles, and in this respect differs from the corresponding muscle in the fore-arm. It is a fairly superficial muscle but is partly covered by the *M. ext. dig. communis*.

Perrin homologizes this muscle with Hoffmann's *M. fibulae metatarsum II* and Humphry's *M. supinator pedis*, admitting the discrepancy between the origin and insertion of the muscle described by the German and English authors and of the one which he himself describes. There does not appear to be a muscle in the Salamander which exactly corresponds with Humphry's *supinator pedis*, perhaps the nearest being the *M. abductor digiti I*. This muscle admittedly arises from the *intermedium*, and not from the fibula, but it is inserted on the metatarsal and is joined to the *M. extensor digiti brevis superior I*. Further, it is definitely a muscle of the deep stratum, while the *rotateur inverse du pied* of Perrin is rather to be associated with the superficial muscles, and in *Cryptobranchus* (*Menopoma*) Eisler figures the muscle as actually arising from the fibula as well as from the *intermedium* (Eisler 1895, Taf. XII, fig. 25, 7 a). The absence of figures in Hoffmann's account renders identification difficult, but there can be no doubt that his description in general has been largely influenced by Humphry's, and that the identification of Hoffmann's *M. fibulae-metatarsum II* with Humphry's *M. supinator pedis* is sound.

It seems, therefore, probable that Perrin's *M. rotateur inverse du pied* is included by Humphry in his 'Tibialis anticus passing to tarsus', and by Hoffmann in his *M. femoro-tibialis*.

Innervation: From N. dorsalis pedis intermedius.

Function: It tends to turn the foot into the supine position.

M. extensor cruris tibialis (m.e.c.t.). Ribbing (1909).

Extenseur tarsien interne + extenseur primitif du tibia Perrin (1892).

Extensor tarsi tibialis brevis + femoro-tibialis superficialis + femoro-tibialis profundus Eisler (1895).

Together with *M. extensor tarsi tibialis* =

Tibialis anticus . Funk (1827); Schmidt, Goddard, and van d. Hoeven (1864); Humphry (1872).

Abductor et flexor pedis + Introflexor pedis (39). Carus (1828).

Femoro-tibialis Hoffmann (1873-8).

Tibialis Osawa (1902); Sieglbaur (1904).

Arising from the *epicondylus lateralis femoris* the muscle is inserted along the whole lateral border of the tibia and extends also to the *tibiale* and *cart. pre-hallucis*, while some of the proximal fibres pass to the mesial side of the *crista tibiae*. It will be noticed that both Eisler and Perrin distinguish between the portion which is inserted on the tarsus and that which is inserted on the tibia, but any such differentiation must be regarded as largely artificial, or at most incipient, in the Salamander.

Innervation: From N. dorsalis pedis intermedius and N. dors. ped. tibialis (N. sphenus).

Function: Extensor of the tibia and leg.

It should be observed that the separation of the pre-axial extensor muscle mass into two is more complete in the hind-limb than in the anterior limb.

MM. extensores digitorum breves (m.e.b.). Eisler (1895); Osawa (1902).

Extensor brevis Carus (1828).

Extensor hallucis brevis + extensor quatuor digitorum brevis
Schmidt, Goddard, and van d. Hoeven (1864).

Extensor brevis digitorum Mivart (1869); Humphry (1872).

Tarsu-digiti I-V Hoffmann (1873-8).

Extenseurs des doigts Perrin (1892).

Extensor digiti I; extensores breves digitorum II-V . Sieglbaur (1904).

Extensores breves superficiales et profundi Ribbing (1909).

Two strata of the digital extensor muscles are distinguishable and will be referred to as 'superficialis' and 'profundus' respectively. They arise generally from the tarsal elements and are inserted by means of a tendon on the base of the terminal phalanx of each finger. Each tendon is also attached to the other phalanges by means of small lateral lips at the inter-phalangeal joints. Hoffmann and Eisler

wrongly describe these tendons as being associated with the *M. ext. dig. communis*. They have nothing whatever to do with this muscle (cf. Sieglbaur and Perrin).

The details of the several digits will be dealt with individually.

MM. abductor et extensor digiti I (m.a.e.1). Sieglbaur.

MM. abductor et extensor hallucis . . . Osawa (1902).

These muscles arise from the dorsal surfaces of the *intermedium* and *centrale* and pass obliquely across the tarsus. The abductor portion is inserted on the lateral face of the metatarsal, while the extensor portion is distinguishable therefrom by its tendinous insertion on the phalanx of the same digit. The abductor portion of this muscle is probably identical with Humphry's *M. supinator pedis* and Hoffmann's *M. fibulae-metatarsum II* (see also p. 111).

The *M. extensor digiti brevis superficialis II* arises alongside the previous muscle from the *intermedium* and *centrale*, and passes across the tarsus to the level of the base of the proximal phalanx of the second digit. Here it passes into a tendon which is inserted on this phalanx, and on the base of the terminal one, in the manner already described.

The *M. extensor digiti brevis superficialis III* arises by two heads: (i) from the *intermedium* together with I and II, and (ii) from the dorsal surface of the fibulare. The two heads pass into a common tendon which is inserted on the bases of the phalanges of the third digit.

The *M. extensor digiti brevis superficialis IV* has a single origin from the fibulare and has the typical insertions on the phalanges of the fourth digit.

The *M. extensor digiti brevis superficialis V* also arises from the fibulare and is inserted on the bases of the phalanges of the fifth digit. It is a relatively slight muscle.

The *MM. extensores digitorum breves profundi* of the several digits arise from the respective basal elements of the tarsus. It is noteworthy, however, that the muscle to the first digit arises from the united basals of the first and second digits and *not* from the cart. pre-hallucis (cf. p. 42). They are all short feeble muscles and are inserted on the dorsal side of the tendons of the corresponding superficial portions at about the level of the distal ends of the metatarsi.

Eisler describes and figures three layers of extensor digiti muscles



for Menopoma, namely, 'superficialis', 'medius', and 'profundus', but the 'medius' layer is indistinguishable in Salamandra.

Innervation: From the NN. dorsalis pedis intermedius and fibularis.

Function: To extend the digits.

M. extensor cruris et tarsi fibularis (m.e.c.t.f.). Ribbing (1909).

Extensor and abductor of the tarsus . . . Rymer Jones (1852).

Peroneus longus . . . Schmidt, Goddard, and van d. Hoeven (1864).

Peroneus . . . Humphry (1872); Osawa (1902); Sieglbaur (1904);
Appleton (1928).

Femoro-tarsali-fibulare + femoro-fibularis . . . Hoffmann (1873-8).

Extenseur tarsien externe (94), Extenseur primitif du fibula (96)
Perrin (1892).

Part of extensor digitorum communis longus + femorofibularis brevis
Eisler (1895).

The superficial and deep strata of the extensor muscle on the post-axial side of the limb are not so easily separable as on the tibial side. They arise together from the epicond. lat. fem. immediately posterior to the M. ext. dig. comm. as well as from an aponeurosis on the post-axial border of this muscle. The superficial fibres—representing the muscle designated by the *first* name in the synonyms of Ribbing, Rymer Jones, Hoffmann, Perrin, and Eisler—are inserted on the *fibulare*, while the deeper fibres are inserted all along the lateral face of the *fibula*.

Innervation: From N. peroneus.

Function: Extensor and abductor of the fibula and post-axial side of the limb.

4. Flexor Muscles of the Leg and Foot (Pl. VIII, figs. 48 and 49).

These should be dissected from the ventral side.

M. flexor primordialis communis (m.f.p.). Ribbing (1909).

Together with M. flexor accessorius lateralis =

Fléchisseur externe des doigts . . . Perrin (1892).

Plantaris superficialis major and minor . . . Eisler (1895).

Plantaris profundus III . . . McMurrich (1904).

Together with MM. flexores accessorii and pronator profundus =

Flexor digitorum sublimis . . . Osawa (1902).

Together with MM. flexores breves superficiales =

Superficial stratum of plantar muscles of leg and foot, s. flexor sublimis
digitorum . . . Humphry (1872).

Together with MM. flexores breves superficiales and flexores accessorii =

Flexor digitorum communis . . . Funk (1827).

Flexor longus (41)	Carus (1828).
Oberflächlicher Beuger	Meckel (1828).
Flexor longus digitorum pedis	Rymer Jones (1852).
Flexor quatuor digitorum communis longus, and flexor hallucis proprius		Schmidt, Goddard, and van d. Hoeven (1864).
Flexor digitorum	Mivart (1869).
Femoro-fibulae-digiti I-V	Hoffmann (1873-8).

This muscle differs somewhat from its counterpart in the anterior limb, since instead of taking its origin entirely from the lateral condyle of the proximal bone of the limb—the *epicond. lat. femoris*—the greater portion of it arises from the distal joint of the limb, viz. from the lateral face of the fibula. The direction of the fibres is approximately parallel with the axis of the limb. In the region of the tarsus the muscle passes into a strong, broad aponeurosis spreading over the sole of the foot—the *fascia plantaris* (fas.pl.) (Eisler). This fascia divides up into five strong tendons which pass along the flexor side of the digits and are inserted in the proximal end of the terminal phalanx of each toe. Where the toe possesses more than one phalanx the tendon is strapped down to the sides of the proximal end of each by means of small lateral slips. The *fascia plantaris* is thus equivalent to the palmar fascia of the hand. It is joined on its ventral—superficial—side by the tendon of the M. ischio-flexorius, while on the dorsal—deep—face the MM. flexorius accessorius medialis and lateralis are inserted, and the MM. flexores breves superficiales originate. It should be noticed that the fibres on the fibular side of the leg are necessarily very short, while those on the tibial side pass along the whole length of the leg.

Both Eisler and McMurrich distinguish from the above described major portion of the muscle a small slip which they respectively call *Plantaris superficialis minor* and *Profundus III minor*. This portion is relatively quite small and arises from the ventro-mesial edge of the fibula immediately proximal to the origin of the M. caput longum musculorum contrahentium. It passes somewhat obliquely to fuse with the major portion on its tibial border. Ribbing, probably more correctly, regards it as a portion of the M. flexor accessorius medialis (see p. 116).

Innervation: Both portions are supplied by the main branch of N. fibularis, and by its R. medianus.

Function: It mainly serves to flex the digits and the tarsus, but, owing to its origin spreading along the whole length of the fibula and the inequality in the length of the fibres on the fibular and tibial sides of the limb, the contraction of the muscle must also tend to

rotate the leg so as to turn the pre-axial side of the limb inwards and caudalwards.

M. flexor accessorius lateralis (m.f.a.l.). Ribbing (1909).

This forms a small sheet of muscle arising mainly from the lateral edge of the *fibulare*, while a few fibres take their origin from the fifth *basale* and from the distal end of the fibula. The fibres pass obliquely tibialwards to about the middle of the tarsus where the muscle is inserted on the *fascia plantaris* of the *M. flexor prim. comm.* Indeed most authors regard it as forming a part of the latter muscle, but, as Ribbing correctly points out, they are clearly separated by the fibular nerve.

Innervation: By the terminal twigs of R. medianus, N. fibularis.

Function: It is accessory to the *M. flex. prim. comm.*, with a distinct pronating action.

M. flexor accessorius medialis (m.f.a.m.). Ribbing (1909).

Fléchisseur interne des doigts Perrin (1892).

Plantaris profundus I, II, et III Eisler (1895).

Plantaris profundus II McMurrich (1904).

Together with *M. pronator profundus* =

Pronator pedis Humphry (1872).

Together with *M. flexor primordialis communis* and *M. pronator profundus* =

Flexor digitorum sublimis Osawa (1902).

Together with *M. pronator profundus* and *MM. flexores breves superficiales* may =

Femoro-fibulae metatarsi I, II, III Hoffmann (1873-8).

This is a larger and more powerful muscle than the former whose fibres run parallel with it and are separated from it by the *M. caput longum musculorum contrahentium*. It arises from the distal two-thirds of the *fibula* on the ventro-mesial aspect of this bone, from the *fibulare*, *intermedium*, and from the *basalia III-V* inclusive. It is inserted over the dorsal surface of the *fascia plantaris* on the tibial side of the *M. flex. acc. lat.*, while its insertion also extends rather more proximally than this muscle.

Innervation: By terminal twigs from R. medianus, N. fibularis.

Function: Like the former muscle it is accessory to the *M. flex. prim. comm.* with a distinct pronating action.

MM. flexores breves superficiales (m.f.b.s.). Eisler (1895); McMurrich (1904); Ribbing (1909).

Fléchisseur de la I, II, III, IV, V phalange; Fléchisseur du I, II, III,

IV, V métatarsien; Fléchisseur de la III, et IV phalangine; Fléchisseur de la IV phalangenette	Perrin (1892).
Flexores digitorum sublimes breves	Osawa (1902).
Together with the M. flex. prim. comm. =	
Flexor digitorum sublimis	Humphry (1872).
Together with flexores accessorii and flex. prim. comm. =	
Femoro-fibulae-digiti I-V	Hoffmann (1873-8).

This series of small muscles correspond very closely with the similarly named muscles of the hand. They arise from the dorsal side of the *fascia plantaris* and from its digital tendons. The details of the several digits vary somewhat as follows:

Digit I possesses one small muscle slip inserted along the tibial border and distal end of the metatarsal.

Digit II has three small fascicles, two lateral inserted on either side of the metatarsal, and a median inserted on the base of the proximal phalanx.

Digit III has five muscle slips recognizable as belonging to this series. These comprise two lateral pairs, one pair inserted on each side of the metatarsal, and the other pair, somewhat smaller, inserted on the base of the proximal phalanx. The remaining slip is a median one and is inserted on the base of the middle phalanx, but although it is a median muscle its insertion is double so as to allow for the passage of the insertion tendon of the M. interphalangeus.

Digit IV is exactly similar to digit III.

Digit V has a very small median slip attached to the base of the proximal phalanx and a pair of lateral muscles inserted on the sides of the metatarsal.

Innervation: All the slips are innervated by twigs from the plantar nerve loop.

Function: To flex the digits.

M. caput longum musculorum contrahentium (m.c.l.c.) Ribbing (1909).

Fléchisseur commun profond des phalanges	Perrin (1892).
Fibulo-plantaris	Eisler (1895).
Flexor digitorum profundus	Osawa (1902).
Fibulo-tarsalis	McMurrich (1904).

Together with the following muscle =

Flexor digitorum profundus	Humphry (1872).
Fibulae-metatarsi et digiti I-V	Hoffmann (1873-8).

This muscle resembles the muscle of the same name in the anterior limb and is narrow and ribbon-like. It arises from the mesial side of

the proximal end of the fibula, and passes directly down the leg to the tarsus, where it merges into a flat transverse tendon which is inserted on the distal row of tarsal bones—the *basalia*. As in the hand, the MM. *contrahentes digitorum* arise in part from this tendon.

Innervation: From N. fibularis, and mainly from its R. medianus.

Function: It is the deep flexor of the tarsus.

MM. contrahentes digitorum (m.c.d.). Ribbing (1909).

Fléchisseurs profonds des phalanges	Perrin (1892).
Flexores breves medii s. <i>contrahentes digitorum</i>	Eisler (1895).
Flexores digitorum profundi breves	Osawa (1902).
Flexor brevis medius	McMurrich (1904).

Together with the former muscle =

Flexor digitorum profundus	Humphry (1872).
Fibulae-metatarsi et digiti I-V	Hoffmann (1873-8).

As already mentioned, this series of small flexor muscles arises partly from the tendon of insertion of M. cap. long. musc. contra., and partly from the *basalia*. The slip going to the first digit is slight and weak, while its direction is very oblique owing to the fact that it arises at the base of the second digit from the fused basale I+II. The slip to the second digit also takes origin from this double basale and from basale III, while the third slip arises from *basalia* III and IV. The fourth slip arises only from basale IV, but the fifth originates from both IV and V. The insertion of each slip is by means of a short tendon on the base of the proximal phalanx of the corresponding digit.

Innervation: By twigs from the plantar nerve loop which pass dorsal to the muscles, thus separating them from the MM. *flexores breves profundi*.

Function: In the case of the first digit the muscle acts mainly as an adductor, and only slightly as a flexor, while in the second, third, and fourth the action is almost purely flexor, and in the fifth toe both adductor and flexor.

M. pronator profundus (m.p.p.). Ribbing (1909).

Pronateur du pied	Perrin (1892 a).
Rotateur direct du pied	Perrin (1892).
Fibulo-tarsalis	Eisler (1895).
Plantaris profundus I	McMurrich (1904).

Together with M. flex. acc. med. =

Pronator pedis	Humphry (1872).
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and probably

Femoro-fibulae-metatarsi I, II, and III . . . Hoffmann (1873-8).

Together with M. flex. prim. comm. and MM. flexores accessorii =

Flexor digitorum sublimis Osawa (1902).

This is the deepest of the three pronating muscles of the leg. It arises from the mesial side of the fibula, deep to the M. flex. acc. med. Its fibres converge towards their insertion on the lateral face of the distal end of the tibia, the tibiale, the cart. pre-hallucis, and the base of the first metatarsal. The muscle is thus triangular in shape.

Innervation: From N. interosseus.

Function: It is the chief pronator of the foot.

M. interosseus cruris. Ribbing (1909).

Pronator tibiae Humphry (1872); Osawa (1902).

Fibulae-tibialis Hoffmann (1873-8).

Interosseus de la jambe Perrin (1892).

Fibulotibialis s. interosseus Eisler (1895).

Interosseus McMurrich (1904).

Like the muscle in the fore-arm this is a thin sheet of muscle joining the mesial sides of the two bones in the distal joint of the limb—in this case the fibula and tibia. It may be regarded as arising from the proximal portion of the fibula and inserted on the distal part of the tibia. It lies deep to the M. pronator profundus as seen from the flexor side.

Innervation: From N. interosseus.

Function: It forms an elastic ligament between the two bones of the leg.

MM. flexores breves profundi (m.f.b.p.). Eisler (1895); Ribbing (1909).

Tarso-metatarsales Humphry (1872); Osawa (1902).

Tarso-metatarsi I-V Hoffmann (1873-8).

Fléchisseurs primitifs des métatarsiens Perrin (1892).

Flexor brevis profundus McMurrich (1904).

These form yet another series of short flexor muscles to the digits. They lie immediately deep to the MM. contrahentes digitorum, and are short, bulky muscles arising from the distal faces of the *basalia*. Each muscle, except that of the first digit, has three insertions, namely, on either side of the corresponding metatarsal and on its ventral face. The lateral insertions extend along practically the whole length of the bone, but the ventral portion does not extend

more than half-way, i.e. as far as the origin of the MM. flexores digitorum minimi. They are necessarily short but nevertheless relatively powerful muscles, the post-axial slip being rather longer than that on the pre-axial side. On the post-axial side of the fifth digit the origin of the muscle extends right back along the side of *basale V*, while a few fibres may even arise from the *fibulare*. In the first digit there is but a single slip which passes obliquely from the composite *basale I+II* to the ventral side of the first metatarsal. This muscle is therefore triangular in shape, and since there is no M. flexor digiti minimus in this digit, its insertion is able to extend along the whole length of the metatarsal.

Innervation: From the plantar nerve loop.

Function: The muscles serve both to flex the tarso-metatarsal joint and in some measure also to approximate the digits.

M. abductor digiti V (m.a.d.5.). Eisler (1895).

Abductor minimi digiti . Schmidt, Goddard, and van d. Hoeven (1864);
Humphry (1872).

Fibulae-metatarsum V Hoffmann (1873-8).

Déducteur du fibulaire + Déducteur du cinquième métatarsien
Perrin (1892).

Abductor digiti quinti Osawa (1902).

Abductor ossis metatarsi quinti McMurrich (1904).

Included in previous muscle by Ribbing (1909).

This is a superficial muscle lying along the extreme post-axial surface of the tarsus. It originates from the distal end of the fibula and is inserted on the post-axial surface of the *fibulare* and *basale V*, and on the base of the *fifth metatarsal*. Its insertion is fleshy.

Perrin distinguishes two muscles according to whether the insertion is on the tarsal elements or on the metatarsal. There does not seem to be any *natural* division of the general muscle mass, however, and therefore such a distinction seems hardly justified.

Innervation: From N. fibularis.

Function: It is the abductor of the fifth toe.

MM. flexores digitorum minimi. Eisler (1895); Ribbing (1909).

Metacarpo-phalangei¹ Humphry (1872).

Metatarso-phalangei Hoffmann (1873-8).

Fléchisseurs primitifs des phalanges Perrin (1892).

Metatarso-phalangeales Osawa (1902).

Flexor brevis profundus (median slips) McMurrich (1904).

These are short muscular slips arising from about the middle of the

¹ An obvious *lapsus calami*.

metatarsals and are inserted on the bases of the proximal phalanges immediately deep to the MM. contra. digit. No representative of this series is present in the first digit.

Innervation: From the plantar nerve loop.

Function: They are the flexors of the first joint of each digit.

MM. interphalangei (m.i.ph.3,4). Eisler (1895).

Phalangei Humphry (1872).

Phalangi I phalanx II digiti III, IV . . . Hoffmann (1873-8).

Fléchisseur primitif de la troisième (quatrième) phalange

Perrin (1892).

Phalangeales Osawa (1902).

Interphalangei III und IV Ribbing (1909).

Two small muscles occur on the third and fourth digits between the proximal and middle phalanges. They have tendinous insertions on this latter bone.

Innervation: From the plantar nerve loop.

Function: They are the flexors of the interphalangeal joint.

MM. intermetatarsales (m.i.mt.). McMurrich (1903).

Interossei metacarpales¹ Humphry (1872).

Interossei metatarsales Hoffmann (1873-8).

Intermétatarsiens Perrin (1892).

Interossei . . . Eisler (1895); Osawa (1902); Ribbing (1909).

These correspond to the MM. intermetacarpales of the hand. They spread web-like across the interdigital space between the metatarsals and can only be seen fully by removing the MM. flexores breves profundi. They extend rather more distally along the fibular side of each metatarsal than along the tibial side.

Innervation: Also from the plantar nerve loop.

Function: They serve to approximate, or adduct the digits.

The limb muscles of *Salamandra* are to be regarded as being in a state of incipient differentiation and specialization. A glance at the lists of synonyms will bear testimony to this fact, since in many cases scarcely any two investigators share the same opinions as to how a given muscle mass should be divided. Thus, while every effort has been made to ensure that these lists shall be accurate and complete, it is not possible to give the exact equivalent in all cases.

It will have been noticed that there is a general agreement between the arrangement of the muscles in the fore- and hind-limbs, particularly in respect of the distal portions of the limbs. One noteworthy

¹ Again obviously a *lapsus calami*.

exception must be mentioned, however, namely, the entire absence in the leg of any muscles corresponding with the *M. flexor antibrachii et carpi radialis*, the *M. flexor carpi ulnaris*, and the *M. flexor antibrachii ulnaris* of the fore-arm. Doubtless correlated with this difference is the fibular origin, in the hind-limb, of the *M. flex. prim. comm.* in addition to its femoral origin, since in the anterior limb this muscle originates from the humerus alone.

It is not possible in the present work to compare the muscles of *Salamandra* with those of related groups or with the *Mammalia*, since such a discussion must necessarily be lengthy, and moreover is to be found in the works of Ribbing mentioned in the Bibliography.

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V

THE NERVOUS SYSTEM

BRAIN AND SPINAL CORD

1. Historical.

FUNK, in his general monograph (1827), describes the external features of the brain, but his figures are poor. In 1890 Oyarzun published some account of the histology of the fore-brain, and a year later Burckhardt gave a very good account of the brains of Triton and Ichthyophis. His work has been used as a basis by most subsequent investigators of the brains of Urodeles. In 1897 Gehuchten discusses the habenular ganglia and commissure. Bochenek (1899) and Rubaschin (1903) add contributions to the histology of the fore-brain, whilst more recently Röthig (1911-27) has made a very careful and extensive study of the constitution of the several parts of the brain of a number of Urodeles, including Salamandra. Drüner (1901) gives excellent figures of the brain of Salamandra, both larval and adult, in his paper on the muscles and nerves of the hyobranchial apparatus, but he does not describe them.

Some five workers have made a special study of the pituitary body, or hypophysis cerebri. The first of these was Haller (1896). His work is very good, and he recognizes that the infundibular portion undergoes considerable atrophy, but fails to differentiate more than one region in the hypophysial part. He was followed by Bochenek (1902), who, working with Golgi's neurological methods, concentrated on the distribution of the fibre tracts within the infundibulum. Haller returned to the subject with a larger comparative account in 1909, but it was not until 1921 that a complete description of the hypophysis was given by Atwell, while three years later a confirmatory account was published by Sumi (1924).

The present account deals only with the general structure and external features, including the main commissures and cavities visible in a median sagittal section. The works above referred to, and others of a more general nature included in the bibliography, must be consulted if further details are required.

2. Membranes of the Brain and Spinal Cord.

Our knowledge of the membranes investing the brain and spinal cord in Urodeles is still far from being adequate. Some account of

them was given by Rex in 1893, in his paper on the blood-vessels of the brain in Triton and Salamandra. Five years later, in 1898, Miss Helen O'Neill made a very careful and detailed study of this subject, taking Salamandra as her type. She describes two membranes, a *dura mater*—of which there are two layers—and a *primary vascular coat*. Later Sterzi in a series of papers (1899–1909) reviews the structure of the meninges of vertebrates in general, and supposes that there is only one primary covering to the brain in Urodeles—the 'Meninx primitiva'—from which may separate a 'Meninx secundaria' (corresponding with O'Neill's primary vascular coat), both of which, in higher animals, give rise to the pia mater and arachnoid. More recently Flexner (1929) has studied the development of the brain coverings in Amphibia in both normal and experimental animals and has come to the conclusion that in Amblystoma (taken as a type of Urodeles) there are *three* membranes investing the brain, the dura mater, pia mater, and arachnoid, and that the last develops from the inner surface of the *dura*.

Thus we are faced with three competent observers describing respectively two, one, and three primary meninges in the adult Urodele. The differences between them are largely those of interpretation of homologies and mode of origin, since each admits *three membranes*.

Miss O'Neill's work was done under the supervision of Professors Wiedersheim and Gaupp and is the most detailed as far as Salamandra itself is concerned. It has been thought advisable therefore to adhere to her interpretation pending a more satisfactory and decisive solution of the whole problem.

Following Miss O'Neill's terminology, the two membranous envelopes surrounding the brain and spinal cord are:

(i) The *dura mater* on the outside. A firm tough membrane, consisting of connective tissue-fibres with flattened cellular elements between them. It is slightly pigmented, the pigment cells being of the stellate variety. In a few special places, to be enumerated later, the dura mater splits so as to form two layers separated by a space, the *interdural space*. The outer layer, next to the bone of the cranium or vertebral column, is the *periosteal layer*; the inner layer, lying nearer to the brain or spinal cord, is the *neural layer*.

(ii) The inner envelope or *primary vascular coat*, which carries the blood-vessels. It lies next to the neural tissue itself and corresponds with the *pia mater* of most authors. According to Miss O'Neill, two layers are distinguishable: namely, an inner, more or less homogeneous, firm layer in which cellular elements

are scarce, and an outer alveolar layer. The blood-vessels lie between the two.

The space between the dura mater and the primary vascular coat is called the *primary subdural space*. It is not a homogeneous cavity, but is filled with a loose vacuolated tissue which Miss O'Neill likens to embryonal 'Schleimgewebe', so that the subdural space in the Salamander is represented by a number of small spaces rather than by a continuous cavity.

Miss O'Neill considers this condition primitive, representing a phase earlier than the formation of a true 'arachnoid' membrane. It should be noted here that, owing to the shrinkage of the neural tissue in the processes of fixing and hardening, whether for section cutting or dissection, the primary subdural space is always seen more or less badly distorted. It is therefore difficult to determine its exact relations with accuracy.

Modifications of the Envelopes surrounding the Brain. The splitting of the dura mater and the formation of an interdural space in certain regions have already been mentioned. This occurs only in the cranium, and does not extend into the vertebral canal. There are four such splits, and they are formed by: (i) the saccus endolymphaticus; (ii) the saccus perilymphaticus; (iii) the pituitary body, or hypophysis cerebri; and (iv) the paraphysis.

(i) *Spatium interdurale endolymphaticum* (O'Neill), as the first is called, is the largest. The *saccus endolymphaticus* is easily seen, on removing the roof of the cranium, lying at the sides of the midbrain, owing to the fact that it is filled with a white chalky material. It is connected with the ear by means of the *ductus endolymphaticus*, which passes through the cranial wall into the auditory capsule. Both Hasse (1873) and Rex (1893) state that it is subdural in position, that is, they imagine that the ductus endolymphaticus penetrates the dura mater and swells out into the saccus endolymphaticus between this envelope and the inner vascular coat. This would put Salamandra—and Triton—in a peculiar position, since, in the Frog, both Coggi and Gaupp had shown the endolymph sac to be *interdural*. Miss O'Neill has demonstrated that this anomaly does not exist, and that in Salamandra the endolymph sac splits the dura into two layers, and is therefore interdural as in the Frog.¹ The dorsal and lateral walls of the endolymph sac are richly vascular, while the mesial wall—the 'pars media' of Hasse—lies very close to the brain and to the plexus covering the fourth ventricle, so that in the region of this plexus the neural layer of the dura and the primary vascular coat are brought

¹ For other views on the position of the saccus endolymphaticus see table on p. 128.

so close together that—according to Miss O'Neill—it is not possible to distinguish between them. In this region also the saccus endolymphaticus is continuous right across the dorsum of the brain and communicates with the sac of the opposite side.¹ Thus the spatium interdurale is also continuous, since it is caused by, and develops *pari passu* with, the development of the saccus. Ventrally the spatium interdurale and the saccus terminate lateral to the pituitary body. The trigeminus nerve passes through the interdural space to the exterior, while the anterior root of the vagus and the acustico-facialis root leave the cranial cavity at the border between the spatium endolymphaticum and the spatium perilymphaticum.

(ii) *Spatium interdurale perilymphaticum* (O'Neill). This interdural space resembles the former in that it is caused by a saccular outgrowth from the auditory organ, but it is much more limited in extent. The *saccus perilymphaticus* lies within the spatium interdurale and is connected with the ear by the *ductus perilymphaticus*, which passes through a special opening in the cranial wall—the *foramen rotundum* of Hasse, or better, the *apertura ductus perilymphatici* (O'Neill).

Hasse thought that the ductus perilymphaticus was connected with the inner envelope of the brain (*Gehirnhülle*), and that the perilymph flowed into the cavum epicerebrale, that is, into the space between the brain and the *Gehirnhülle*. Miss O'Neill, on the other hand, is convinced that this is not the case, but that the perilymph is confined to the saccus perilymphaticus within the interdural space. In this she is supported by Harrison (1902). She thinks, however, that there may be, here and there, some connexion between the perilymph and the endolymph where the two sacs come into close contact.

The spatium interdurale perilymphaticum lies ventral to the spatium interdurale endolymphaticum which is laid over it like a saddle, extending beyond it anteriorly and posteriorly.

(iii) *Spatium interdurale hypophyseos* (O'Neill). As is well known, the hypophysis cerebri or pituitary body develops as an evagination from the roof of the mouth, and finally separates entirely therefrom, becoming applied to the ventral surface of the brain at the infundibulum. In doing this it passes through the periosteal layer of the dura mater and pushes the neural layer in front of it, thus forming and lying within an interdural space—the spatium interdurale hypophyseos.

¹ Dempster (1930) states that while the two sacci endolymphatici do communicate in some Urodeles they do not do so in Salamandra, where they abut very closely and are separated only by an exceedingly thin membrane. He accepts Sterzi's view as to their position, but does not mention Miss O'Neill's paper.

So close does the hypophysis lie to the infundibulum that Miss O'Neill states she is unable to detect the neural layer of the dura mater between them, and therefore suspects that at this point the interdural space and the subdural space may actually communicate with one another.

(iv) *Spatium interdurale paraphyseos* (O'Neill). The fourth interdural space is a median dorsal one. The paraphysis is a dorsal outgrowth from the roof of the thalamencephalon (see under 'Brain'), and as it comes into contact with the dura mater during its development, it penetrates the neural layer and spreads out between this layer and the periosteal layer, thus producing a space between them. It will be noticed that this space is produced in exactly the same manner as those already described, but in the reverse direction, namely, by a centrifugal outgrowth instead of a centripetal one. Since the paraphysis remains attached to the brain, the spatium interdurale paraphyseos retains a communication with the subdural space.

The *primary vascular coat* of the brain entirely envelops this important organ. It takes part in the formation of the several plexuses—see 'Vessels of the Brain'.

Modifications of the Envelopes surrounding the Spinal cord. There is little or no splitting of the dura mater, with the consequent formation of an interdural space, within the vertebral column. The only sign of such a condition is towards the anterior end, where the V. post-occipitalis passes through the dura on its way out from the vertebral column.

On the other hand, there are three well-defined thickenings of the primary vascular coat.

Two of these, forming a pair of longitudinal bands running one on either side of the spinal cord between the dorsal and ventral nerve roots, were first described by Berger in 1878. He called each the *ligamentum denticulatum*. They commence at the level of the second vertebra and continue right down the body, protruding a little distance into the subdural space and are suspended by a reduplication of the vascular coat.

The third thickening of the primary vascular coat is situated in the mid-ventral line beneath the *sulcus longitudinalis ventralis*, and forms the *ligamentum piae ventrale* (O'Neill). The spinal cord is somewhat eccentrically placed in the vertebral canal, being rather nearer the ventral side. This brings the ligamentum piae ventrale into very close connexion with the dura mater, and interrupts the subdural space mid-ventrally.

Comparison of the three interpretations of the meningeal coverings

O'Neill (1898)	Sterzi (1899-1909)	Flexner (1929)
Dura mater:		
(a) periosteal layer	'Endorachis' (periosteum)	Dura mater
(b) neural layer	Meninx primitiva	Arachnoid
Interdural space	Epidural space	Subdural space
Primary vascular coat	Meninx secundaria	Pia mater
Saccus endolymphaticus	Saccus endolymphaticus	Saccus endolymphaticus
<i>inter-dural</i>	<i>epi-dural</i>	<i>sub-dural</i>

3. Brain (*gross anatomy only*) (Pl. IX).

The brain of the Salamander is very long compared with its breadth and depth—a feature typical of Urodeles in general. Its length, from the anterior end of the hemispheres to the origin of the first spinal nerve, is approximately 14 mm.; its breadth, measured across the posterior part of the hemispheres, is about 4 mm.; while its depth, from the roof of the mesencephalon to the infundibulum, is only some $3\frac{1}{2}$ mm.

In *dorsal* view (Fig. 51), the following features are conspicuous:

(i) The *olfactory lobes*. These are not fused into a median, unpaired body as in the Frog, but are lateral structures which merge, without any sharp line of demarcation, into

(ii) The *hemispheres* of the *prosencephalon*, or *telencephalon*. These are long, cylindrical bodies with rounded ends. Together with the olfactory lobes they form about 37·5 per cent. of the total length of the brain, their diameter being greatest at about two-thirds their length from the anterior end. They lie very close to each other anteriorly, but their posterior ends turn slightly outwards from the middle line. The telencephalon is followed posteriorly by:

(iii) The *diencephalon*. The anterior portion of this section—the *thalamencephalon*—is scarcely visible from the dorsal side, being covered by the triangular nodus chorioideus and its associated *paraphysis*. The paraphysis develops from the anterior wall of the thalamencephalon as a dorsal evagination and becomes associated with a rich vascular plexus, forming the *nodus chorioideus*. In the adult the tissue of the paraphysis is largely confined to the posterior region of the plexus. It does not penetrate the cranium but is flattened out against its roof. The anterior portion of the roof of the diencephalon appears at first sight to possess a median cleft. Close inspection, however, reveals a weak bridge of nervous material, the *habenular com-*

missure, followed by a clearer area—the *pulvinar*. It is from the posterior end of this region that the *epiphysis* (epi.) and its terminal *pineal body* evaginate. They are only weakly developed in the Salamander and never perforate the cranial roof, but flatten out over the surface of the brain between it and the parietals. In the adult the epiphysis becomes very closely applied to the surface of the brain, but is distinguishable in sections (see Fig. 50). Eycleshymer (1892) states that the paraphysis and epiphysis in Urodela never come into close relation as in Reptilia, but remain widely separated. The condition in the Salamander supports this statement.

(iv) The *corpus opticus* (lob.op.) or *mesencephalon* follows. It is not divided into two distinct lateral lobes as in the Frog, but expands gradually from the roof of the diencephalon into a more or less hemispherical dome. There is a faint groove in the middle line and the nervous tissue is thinner there than elsewhere, this feature being more obvious in transverse sections. The corpus opticum is far removed from the cerebrum. At the posterior border of the mesencephalon there is a deep groove between this and the subsequent portion of the brain, and from this groove the N. trochlearis (fourth cranial nerve) emerges.

(v) The *cerebellum* (cerb.) or *epencephalon* is a very narrow transverse band of nervous tissue forming the anterior boundary of the fourth ventricle, and separated from the mesencephalon by the groove above mentioned. This region is surprisingly slender, being much smaller comparatively than the corresponding region in the Frog.

(vi) The *medulla oblongata* (med.ob.) or *myelencephalon* is a fairly long (about $6\frac{1}{2}$ mm.) shallow trough of nervous tissue, open dorsally. It forms about 42 per cent. of the total brain length. Its anterior end is laterally expanded, and tapers gradually into a more or less circular cross-section posteriorly, merging imperceptibly into the spinal cord. Its cavity—the fourth ventricle—is roofed over dorsally by a rich vascular plexus. The trigeminus (Vth) root arises ventro-laterally from its anterior angles, and the acustico-facialis (VIIth and VIIIth) root appears about $\frac{3}{4}$ mm. posterior to this. The glossopharyngeus-vagus complex (IX and X) arises laterally from the sides of the medulla by three roots, of which the middle root is the largest, the other two being very fine.

The following additional features are evident on the *ventral* surface of the brain (Fig. 52):

(i) The emergence of the *olfactory nerves* (n.1) from the brain.

They are not quite terminal, but arise ventrally a short distance from the anterior end of the prosencephalon.

(ii) The floor of the *thalamencephalon* (thc.) fits in as a wedge between the hemispheres, which are to be regarded as lateral outgrowths from it.¹ The *optic nerves* (n.2) pass from its floor at about the level of the posterior ends of the hemispheres.

(iii) The *infundibulum* (inf.) is an outgrowth from the floor of the *diencephalon* which extends in a postero-ventral direction so as almost to obscure the floor of the *mesencephalon*. Its posterior end is somewhat expanded laterally and has a fairly deep median notch. Transverse sections show that the neural tissue is almost entirely confined to the ventral surface, its roof being very thin and membranous. In sagittal section it appears as a hollow wedge. From the posterior angles of the median cleft the pituitary body is suspended.

(iv) The *pituitary body* (pit.), or hypophysis cerebri, is roughly a broad oval in surface view, with a median notch anteriorly. The lobes at the sides of the notch are distinguished as the *pars tuberalis* (Atwell) (pit.''), while the main mass is the *pars anterior*. According to Sumi the *pars tuberalis* arises rapidly at about the time of metamorphosis. In many Urodeles it becomes completely detached from the *pars anterior*, but in *Salamandra* its separation is only partial. Both the pituitary and the infundibulum lie within the basi-cranial fontanelle of the primary chondrocranium, and are covered ventrally by the parasphenoid bone.

(v) The ventral surface of the *medulla* calls for no special comment save that the roots of the *trigeminus* and *acustico-facialis* are here more distinct, and the *N. abducens* (VI) is also visible. It arises on either side, very close to the middle line, by two roots about a millimetre posterior to the *acustico-facialis*. It is an exceedingly fine nerve and readily broken, and even when intact it is not easy to see.

In lateral view it should be noted that there is only a very slight departure from the straight unflexed condition of the embryonic brain.

By direct observation of the sagittal section (Fig. 50) it is not possible to make out more than the main features. If the half of the brain is immersed in a solution of ferric chloride the iron salt will be found to adhere more readily to the grey matter than to the white, and thus render the outlines of the cavities more distinct. The positions of the commissures have been confirmed, and in some cases determined, by the help of transverse sections examined microscopically.

¹ Cf. Graham Kerr on the brain of *Lepidosiren*, *Q. J. M. S.*, London, vol. 46, p. 448.

In addition to the commissures and the thickness of the walls of the brain in its various parts, the chief features of interest in a sagittal section are:

(i) The *foramen of Monro* (fo.M.) connecting the *lateral ventricles*—the cavities of the cerebral hemispheres—with the *third ventricle*—the cavity of the thalamencephalon. This is a long oval slit of relatively large dimensions, and through it the blood-vessels pass from the nodus chorioideus to the lateral plexus of the first ventricle.

(ii) The remainder of the pituitary body may now be distinguished:

(a) The *pars intermedia* (Atwell) (pit.'). This is very small, and lies dorsal to the *pars anterior* and behind the infundibulum.

(b) The *pars anterior* (pit.") is bi-convex in section. It forms by far the largest portion of the gland.

(c) The infundibular portion, or *pars posterior*, shows considerable retrogression and is almost non-existent.

(iii) The purely epithelial portions of the brain surface are as follows:

(a) The *lamina terminalis* (lam.ter.) and antero-dorsal roof of the thalamencephalon.

(b) The dorsal wall of the infundibulum.

(c) The posterior median portion of the mesencephalon.

(d) The roof of the fourth ventricle.

With regard to the commissures on the floor of the foramen of Monro, the upper bundle was first homologized with the *corpus callosum* by Osborn (1886). It had previously been thought to be homologous with the *pars olfactoria* of the anterior commissure, but Osborn showed that this part was present in the lower bundle of fibres as well as the *pars temporalis*, and thus the lower bundle is the entire *anterior commissure*.

SUMMARY.

The brain of the Salamander is straight, or very slightly flexed, and small compared with that of the Frog, but long in comparison with its breadth and depth. The pineal organ is much reduced, while the paraphysis shows considerable development. The separation of the optic lobes is very incomplete and the cerebellum poorly developed. The olfactory lobes are paired and not fused to form a median body as in the Frog. The foramen of Monro is large.

4. Spinal cord.

The medulla oblongata merges imperceptibly into the *spinal cord*, which passes right along the body to the tip of the tail, passing through the neural canal of the vertebral column. It remains fairly uniform in diameter as far as the sacral region, where a slight swelling is noticeable in that part of the cord giving off the sacral nerves. From this point to the tip of the tail the cord gradually diminishes in size.

Segmental nerves are given off corresponding with each vertebra, and arise, with the exception of the first, by both dorsal and ventral roots. The details of their course and distribution will be considered in a subsequent section.

In transverse section the spinal cord is eccentrically placed in the neural canal towards the ventral side. It is approximately oval in shape with a small central canal lined by epithelium, around which is grouped the grey matter. The white matter lies towards the periphery of the cord. There is a well-marked V-shaped groove dorsally—the *dorsal fissure* or *sulcus longitudinalis dorsalis*. It is shallow, however, and does not extend far in a ventral direction. The *ventral fissure*, or *sulcus longitudinalis ventralis*, is much deeper and reaches nearly to the central canal. It is particularly noteworthy that the A. spinalis ventralis lies well within the ventral fissure, thus tending to open it still farther.

CRANIAL NERVES (Pl. X)

1. Historical.

The earlier workers, e.g. Funk and Rusconi, have very little to say with regard to the cranial nerves. In 1840 Vogt gave an account of the vagus nerve and hypoglossal which, however, is not very accurate. Three years later Fischer (1843) published an adequate description of all the cranial nerves except the IVth, which he failed to find. He did not observe the branch from the oculomotorius to the M. rectus superior—in fact he states definitely that it does not exist. He also omits any description of the branchial branches of the Xth nerve. Apart from these omissions he is surprisingly accurate, and is frequently more correct than some of his successors. In the same year Bendz (1843) published an account of nerves IX, X, and hypoglossus, but his work contains a number of errors and is not so accurate as that of Fischer.

In 1891 von Plessen and Rabinowicz gave a description of the

cranial nerves of the larval Salamander based on the study of serial sections, and produced elaborate figures reconstructed from these sections. While these authors rectify Fischer's defective account of the N. oculomotorius they have nevertheless failed to identify the lateralis system which exists in the larval Salamander. The anterior ganglion of this system lies just dorsal to the Gasserian ganglion. They therefore regard it as an accessory trigeminal ganglion and describe the nerves emerging from it as trigeminal nerves. This has naturally led to considerable confusion of nomenclature and description, and a similar confusion exists between the lateralis nerve and its course in the vago-glossopharyngeal ganglionic complex.

These authors also describe and figure an anastomosis between the R. palatinus VII and their R. supramaxillaris superior of the Vth nerve, which does not exist, while they fail to mention the one which does occur between the palatine branch of the VIIth and the ventral branch of R. ophthalmicus profundus V.

The confusion with regard to the lateralis system was cleared up by Strong in 1895, but this author is himself in error when he suggests that the anastomosis between the Vth and VIIth nerves should be between R. palatinus VII and R. maxillaris V. He says: 'In Wiedersheim's *Grundriss* this connexion is in one place, by some error, spoken of as between R. palatinus and R. ophthalmicus profundus.' Actually Wiedersheim is quite right, the difference between the topographical relations of this anastomosis constituting an important distinction between the Urodela and Anura. In 1896 Kingsley re-examined the question of this anastomosis by means of sections, and shows the true communication to be between the palatine and the ophthalmicus profundus, and suggests further that von Plessen and Rabinowicz mistook the M. obliquus inferior for an anastomosis between a branch of the palatine and their R. supramaxillaris superior V.

In 1901 Drüner gave an excellent account, illustrated by a number of fine figures, of the visceral nerves (VII, IX, and X), and of the muscles they supply. His work is very accurate.

A year later Hoffmann published a general account of the cranial nerves of Salamandra and Triton, both larval and adult. His work in respect of the visceral nerves is not so detailed as that of Drüner. While on the whole Hoffmann's account is accurate, his text is not very easy to follow, probably on account of the absence of any diagrams or figures other than those of microscopic sections. Frequent reference to both these papers will be made in the ensuing pages. At about the same time several American anatomists began to investigate

the cranial nerves of their native Urodeles by means of serial sections, paying particular regard to the distribution of their several components. These accounts, notably that of Coghill (1902) for *Amblystoma*, have been found to be of considerable use in unravelling the intricacies of the nerve relations in the head of the Salamander. After making due allowance for the absence of a lateralis component in the adult Salamander, the correspondence between the cranial nerves of this animal and those of *Amblystoma* is very close indeed.

The present account is based almost entirely on observations made by actual dissection carried out under a binocular dissecting microscope—checked in a few cases by microtome sections. No attempt has been made to elucidate the components of the various nerves, but these may be deduced by analogy from the descriptions of American Urodeles above referred to, and the composition of each nerve thus deduced has been given in parenthesis. It should be noted further that where the words 'origin' and 'root' are used they refer only to the point of emergence of the nerve from the surface of the brain and not to the deeper origin within it.

All cranial nerves are paired, and those of one side only are described.

2. Description.

I. N. Olfactorius (n.1). The first cranial nerve leaves the olfactory lobe of the prosencephalon from its ventro-lateral border and passes directly forwards, through the fenestra olfactoria, into the nasal capsule. It is a flat oval in transverse section. Almost immediately after separating from the brain the nerve gives off a branch from its ventral side which turns sharply outwards towards the internal narial opening, and apparently supplies Jacobson's gland. The main olfactory nerve then divides into a dorsal and ventral branch, each of which ramifies over its respective surface of the nasal sac, supplying the olfactory epithelium.

II. N. Opticus (n.2). The optic nerve passes from the floor of the thalamencephalon and is inclined slightly anteriorly and dorsally. It leaves the cranial cavity by the optic foramen in the side wall of the cranium. Since the nerve occupies only a very small part of this 'foramen' it would perhaps be more correct to call the latter the optic fenestra. The nerve is protected within the fenestra, and during its passage from the side of the skull to the bulbus oculi, by a strong, fibrous, connective tissue sheath, the whole structure forming the *optic peduncle*.

Eye-muscle Nerves (Pl. XIII, fig. 57).

In addition to the general accounts already referred to, Schwalbe in 1879 published a description of the eye-muscle and ciliary nerves. He, like Fischer, fails to find the oculomotor branch to the *M. rectus superior*, but he disagrees with him in that he does sometimes find a *N. trochlearis* to be present. He is the first to give an account of the ciliary nerves, both superior and inferior, although he is a little uncertain of the exact relations of the latter.

Owing partly to the small size of the animal, and partly to the rather large amount of individual variation met with, the investigation of these nerves in the Salamander is by no means easy, but with care they may be followed fairly satisfactorily with the aid of a binocular dissecting microscope.

III. N. Oculomotorius (n.3) (somatic motor). The IIIrd nerve leaves the brain from the floor of the mesencephalon and passes out of the cranial cavity through a special foramen—*For. oculomotorium*—in the side wall of the cranium, just posterior to the optic fenestra. Within the orbit it divides into two rami.

(a) A *ramus superior* which turns dorsalwards and enters the *M. rectus superior* along its anterior border.

(b) A *ramus inferior* which passes ventralwards, posterior to the optic nerve, between it and the *M. retractor bulbi*, and close to a branch of the Vth nerve. It divides into three branches, going respectively to the inferior and anterior rectus muscles, and to the inferior oblique muscle. Throughout its course it keeps close to the trigeminal branch above mentioned, and apparently passes across, or through it, above the *M. rectus inferior*.

(c) Close to the point where the *N. oculomotorius* divides into superior and inferior rami a *ramus communicans* to the *R. ophthalmicus profundus* V may be found (n.3-5), and usually at about the same point a slight swelling of the nerve represents the *ciliary ganglion*. Schwalbe (1879) reports several patches of ganglionic cells along the course of the *ramus inferior*, of which the largest is in the position indicated above. Hoffmann (1902) also confirms the presence of ganglia associated with the oculomotor nerve, but says that they surround the nerve like a sheath and are not within the nerve itself, while he considers them to be of a sympathetic nature and to represent the most anterior ganglion of this system. Coghill finds in *Amblystoma* that the ciliary ganglion is transitory, and tends to disappear in the adult. Hence he concludes that it is at no time functional.

It is certain, however, that a ganglion does normally occur associated

with the oculomotor nerve in the Salamander, and it is probably of a sympathetic character, and is not connected with the fibres of the nerve itself. The present investigation has, however, not revealed its exact relations (cf. p. 183).

(d) Both Schwalbe and von Plessen and Rabinowicz state that the oculomotor nerve sends a branch into the M. retractor bulbi. Now while a twig has been found which leaves the nerve together with, or close to, the ramus communicans ad V, passing amongst the fibres of the above-named muscle towards the bulbus, it is improbable that it terminates within the muscle, but seems rather to pass to the eye itself and enter the sheath surrounding the optic nerve. Gaupp reports a similar twig in the Frog. It may be that this nerve is of a sympathetic nature and is associated with the ganglion above referred to, but on this point there is no definite evidence.

The above account agrees fairly closely with Coghill's 'Case A' and appears to represent the most usual arrangement, although individual variations are quite common. They chiefly concern the mode of branching, and the relations between the ramus inferior and the trigeminus branch, and the exact position of the ciliary ganglion.

IV. N. Trochlearis (n.4) (somatic motor+sensory fibres?). The exact relations of this nerve are exceedingly difficult to determine by dissection, partly on account of the fineness of the nerve itself and the toughness of the tissue in which it is embedded, and partly on account of its great variability, even on opposite sides of the same animal. The discrepancies between the several published accounts testify to this.

As above mentioned, Schwalbe was the first to recognize its existence, but in spite of his account von Plessen and Rabinowicz state that the M. obliquus superior is innervated by the trigeminus. Hoffmann (1902) gives a detailed description of the nerve, but describes two anastomoses with the Vth nerve, whereas only one has been found.

So far as the present author has been able to observe, the most usual arrangement is as follows. The nerve leaves the brain near the middle line immediately in front of the cerebellum, emerging on the dorsal side from the deep groove which exists between this part of the brain and the corpus opticus. The nerve passes antero-laterally through the cranial cavity, and in doing so is often closely applied to the under-surface of the parietal bone, so that great care must be exercised in removing the roof of the skull to avoid damaging the nerve. It emerges from the cavum cranii through a very oblique foramen in the parietal, or between the parietal and the orbito-

sphenoid (cf. Gaupp, 1911), at about the level, or just in front of, the optic nerve and dorsal to it. The nerve may divide within the skull and pass through its wall as a double nerve, otherwise it divides immediately on emerging from its foramen, and before penetrating the origin of the M. levator bulbi. The division is unequal, one branch being very much finer than the other. The finer branch (IVb, Hoffmann) passes at once through the origin of the M. levator bulbi, and goes to the M. obliquus superior without anastomosing with any branch of the trigeminal nerve. It may come into contact with such a branch but it is comparatively easily separable from it, and no exchange of fibres appears to take place. The larger branch usually turns a little anteriorly before penetrating the origin of the M. lev. bulbi, and after it has emerged from this muscle it always comes into contact, and apparently anastomoses with, one or more cutaneous twigs of the R. ophthalmicus profundus V. It may divide into several twigs, some of which anastomose with branches of the Vth nerve while others pass to the M. obl. sup., or it may anastomose as a whole with a branch from the trigeminus, in which case fibres arise from the combined nerve and enter the superior oblique muscle.

The above description agrees fairly well with that given by Hoffmann, except that no anastomosis between the trochlearis and the trigeminus *mesial* to the M. lev. bulbi such as he describes has been found, neither in fact has any branch of the Vth nerve been found which could fuse with it in this position. It should be noted here that Coghill (1902) describes the trochlearis of *Amblystoma* meeting a trigeminal branch *mesial* to the M. lev. bulbi. He says, 'I find no positive evidence of an anastomosis in this case although the nerves are in very intimate relation with each other. The fourth nerve is penetrated by the trigeminal twig and then passes through the M. lev. bulbi and innervates the M. obliquus superior.' This author, however, does not describe any fusion of the two nerves *lateral* to the M. lev. bulbi, nor any division of the trochlearis into two distinct rami such as occurs in *Salamandra*.

From the above details the following facts emerge:

(i) A N. trochlearis does occur in *Salamandra* and the M. obliquus superior is innervated by it.

(ii) The whole of the fourth cranial nerve is not distributed to the eye muscle, but some part of it goes to the skin or underlying tissues via the track of a trigeminal twig.¹

¹ If Hoffmann's account is correct these apparently cutaneous branches of the trochlearis may actually come from the fifth twig, which, according to him, joins the trochlearis *mesial* to the M. levator bulbi.

(iii) The trochlearis normally divides into two distinct rami, one of which anastomoses with the Vth nerve while the other does not.

Before the significance of these facts can be adequately appreciated a complete reinvestigation of the internal origin and development of this nerve would be necessary.

VI. N. Abducens (n.6) (somatic motor). This is one of the finest of all the cranial nerves and one of the most difficult to investigate. It arises by two roots from the ventral surface of the medulla very far back—in fact posterior to the origin of the IX–X complex—close to the mid-ventral line, and passes anteriorly and laterally alongside the internal carotid artery, leaving the cranial cavity by a special foramen—For. abducentis—just a little antero-mesial to the palatine nerve. It enters the orbit mesial to the M. retractor bulbi. In the adult Salamander the N. abducens is always quite distinct throughout the whole of its course from the trigeminus, and from the Gasserian ganglion, although, according to Hoffmann, it approaches the latter fairly closely in the larva, while in some Urodeles, e.g. Triton, it actually enters the ganglion and leaves it in company with true trigeminus fibres. It supplies the MM. retractor bulbi and rectus posterior, and in order to reach the latter muscle the nerve frequently bifurcates and passes round either side of the M. retractor bulbi, supplying it with numerous fibres on the way, or it may remain entire and pass round the lateral aspect of the retractor muscle.

So far as the present investigation goes, the MM. retractor bulbi and rectus posterior of the Salamander are only supplied by the abducent nerve which is distributed to these muscles alone.

V. N. Trigeminus (n.5). The Vth nerve of the Salamander is probably the most complicated of the cranial nerves. It possesses the typical three branches which, however, are not quite typical in composition, as will be seen later. The nerve arises from the antero-lateral angle of the medulla, and passes immediately into the *foramen pro-oticum* situated just in front of the auditory capsule which is formed by the junction of the trabeculae with the roof of the ear capsules. Within this foramen lies the large *Gasserian ganglion* from which the branches of the trigeminus nerve arise.

Von Plessen and Rabinowicz describe two ganglia in connexion with the Vth nerve; (i) an accessory (Neben-) ganglion associated with a dorsal root, and (ii) a main (Haupt-) ganglion with a ventral root. Now their 'Nebenganglion' is really the ganglion belonging

to the lateralis system and has nothing to do with the trigeminus system at all, it being a larval structure which disappears at metamorphosis. The only trace of this system of nerves to be found in the adult is a very fine connexion between the acustico-facialis ganglion and the Gasserian ganglion—the remains of the Radix dorsalis of von Plessen and Rabinowicz—the whole of the ganglion with its R. ophthalmicus superficialis VII (R. frontalis, v. P. and R.), R. buccalis (R. supramaxillaris superior, v. P. and R.), and R. mandibularis externus (R. buccalis, v. P. and R.) having atrophied, with the possible exception of a few fibres distributed to the skin above the M. levator mandibulae which may represent the remains of the R. ophthal. super. VII (cf. Drüner, 1901, p. 537).

We may now consider the three main rami of the Vth nerve.

V₁. *R. ophthalmicus profundus* (m.5a) (general cutaneous). (See also Pl. XIII, fig. 57.)

R. nasalis	von Plessen and Rabinowicz.
R. ophthalmicus	Hoffmann.

Comparing this ramus with the typical Selachian arrangement, it probably represents both the ophthalmicus profundus and at least a portion of the ophthalmicus superficialis V of that group, but since almost the whole of the nerve passes ventral to the M. rectus sup. it seems justifiable to apply the term 'profundus' to it.

After leaving the ganglion it passes out from the For. pro-oticum, lateral to the orbito-sphenoid cartilage s. trabecula, but *mesial* to the ascending process of the quadrate. (It is thus separated by this process from the other two trigeminal branches.) It then passes directly anteriorly, mesial to the levator muscles of the mandible, between the R. sup. and the R. inf. of the N. oculomotorius, ventral to the M. rectus superior, dorsal to the optic nerve, and between the eyeball and the skull. During its passage through the orbit it gives off several—usually three—branches to the skin on the dorsum of the head. There is a great deal of individual variation in the precise arrangement of these branches, but the following seems to be the one most generally met with. It differs slightly from that given by Hoffmann, but the difference is more apparent than real, as this author seems to be describing one particular case as if it were a rigid plan adhered to by all individuals.

(i) The first branch ($V^{1a1} + V^{1a2}$, Hoffmann) probably represents the R. temporalis superior (Gaupp) of the Frog. It arises from the main stem before it crosses the N. oculomotorius. It passes dorsal

to the M. rectus superior, and immediately above the muscle it gives off:—

(a) The *superior ciliary nerve* (n.cil.s.)—a fairly large branch which either passes over, or through, the muscle and penetrates the sclerotic coat of the eyeball. This would appear to be the V^{1a} of Hoffmann.

(b) The rest of the nerve—Hoffmann's V^{1a2} —which is distributed to the skin overlying the postero-mesial portion of the orbit.

It would seem to be this nerve that the earlier authors described as supplying the M. rectus superior.

(ii) Just *ventral* to the superior rectus muscle a fairly large branch arises which almost immediately divides into two—Hoffmann's V^{1a3} . Both branches pass dorsal to the M. obliquus superior and are distributed to the skin covering the fronto-ethmoidal region, and thus would appear to be the equivalent of the *RR. frontales et palpebrales superiores anteriores* (Gaupp) of the Frog.

These branches very frequently receive an anastomosis from the previous branch, which passes ventral to the M. rectus superior.

(iii) From the ventral side of the main profundus nerve, just posterior to the optic nerve, the *inferior ciliary nerve* (n.cil.i.) is given off. It passes between the optic nerve and the M. retractor bulbi and receives (or gives?) a fine anastomosis from the oculomotor nerve. With this anastomosis are associated both the nerve which runs parallel with the optic nerve to enter the eyeball (see also under N. oculomotorius) and the *ciliary ganglion*.

The inferior ciliary nerve then proceeds lateralwards together with the oculomotor, keeping dorsal to the M. rectus inferior. The nerves cross one another above this muscle, and the inferior ciliary nerve continues in a lateral direction, penetrates the muscle to the ventral side, and then enters the sclerotic coat of the eyeball near the insertion of the muscle.

Just after penetrating the muscle it gives off a branch which passes anteriorly over the floor of the orbit, and is distributed to a small section of the skin of the upper jaw between the most anterior branch of the maxillary nerve and the most posterior twig of the lateral terminal branch of the profundus.

Terminal branches of the profundus ($V^{1c} + V^{1d}$, Hoffmann).

A little anterior to the point where it crosses the optic nerve the ophthalmicus profundus divides into three main terminal branches—mesial, lateral, and ventral. These may anastomose variously with one another until the anterior limit of the orbit is reached. They all

pass ventral to the M. obliquus superior, and dorsal to the M. obliquus inferior.

(iv) *Mesial branch* (V^{1c} , Hoffmann). The mesial terminal branch (n. 5a.M.) passes through the Foramen orbito-nasale mediale in the antorbital cartilage slightly dorsal to the origin of the M. obliquus superior. On entering the nasal capsule the nerve turns mesially and then anteriorly, passing over the nasal sac dorsal to the olfactory nerve. At a point a little posterior to the level of the external nares it breaks up into several fine terminal twigs which penetrate foramina in the premaxilla and the nasal bone, and supply the skin of the snout.

Just before this branch enters the For. orbito-nasale mediale, while it is still within the orbit, it gives a small lateral branch which fuses with a twig from the lateral terminal branch and then enters the nasal capsule separately from the main nerve. It passes dorsal to the nasal sac, and turns first mesially, then sharply laterally, and finally perforates the nasal capsule laterally to supply the skin near the ductus naso-lacrimalis.

The branch just described is composed of fibres from both lateral and mesial terminal branches in varying proportions, and although its course is somewhat peculiar its presence seems to be reasonably constant.

(v) *Lateral branch* (V^{1d} , Hoffmann). The lateral terminal branch (n. 5a.L.) gives off one or two small twigs within the orbit which turn sharply lateralwards, and supply the skin over the upper jaw near the anterior angle of the orbit. The main nerve then itself turns lateralwards, penetrates the For. orbito-nasale laterale, and enters the postero-lateral corner of the nasal capsule. It crosses the corner of the capsule obliquely, more or less lateral to the olfactory epithelium, and passes through the fenestra infraconchalis and then through foramina in the maxilla to supply the skin of the face laterally of the nasal capsule.

(vi) *Ventral branch* (V^{1d} , Hoffmann). The ventral terminal branch (n. 5a.V.) enters the nasal capsule by the For. orbito-nasale mediale directly between the origins of the superior and inferior oblique muscles, a little ventral to the mesial terminal branch, and close to the floor of the capsule. After passing through the foramen the nerve remains entirely ventral to the olfactory epithelium and, turning slightly mesially, anastomoses with the R. palatinus VII just mesial to the internal narial opening. In sections ganglionic cells are discernible at the point where these two nerves join, and even in dissections a swelling suggestive of a ganglion is noticeable. The nerves resulting from this fusion are of course mixed, and contain both

trigeminus and facialis fibres, so that it is not possible to determine the precise distribution of each component by dissection. In general they spread over the roof of the mouth under the nasal organs (see also description of *R. palatinus* VII).

V₂. *R. maxillaris* (n.5b.) (mixed, general cutaneous, and visceral motor).

R. supramaxillaris inferior von Plessen and Rabinowicz.

R. maxillaris superior Hoffmann.

(In the larva this nerve is combined with a lateral line nerve—*R. buccalis* VII—to form the *truncus infra-orbitalis*.)

After separating from the Gasserian ganglion the maxillary nerve enters the antrum petrosum laterale (Drüner) from which it emerges between the processus ascendens and the processus oticus of the quadrate, and passes, mesial to the *M. levator mandibulae externus*, to the posterior angle of the eye. Here it divides into:

(i) The *superior palpebral nerve* (n.s.palp.), (*R. dorsalis*, Hoffmann), ('accessory twigs' of the trigeminus, Coghill), which consists of one or two fairly strong branches supplying the skin of the upper eyelid and also part of that covering the levator mandibulae muscle and ear-capsule. The terminal twigs from these nerves appear to anastomose with those from the superficial branches of the ophthalmicus profundus V.

(ii) An *inferior palpebral nerve* (n.i.palp.) (with the remainder of the nerve = *R. ventralis*, Hoffmann) which supplies the skin of the lower eyelid.

(iii) A very fine motor branch to the *M. levator bulbi* which usually arises between the two palpebral nerves.

(iv) The *maxillaris nerve* (n.max.) proper, of mixed constitution. This nerve passes round the orbit somewhat lateral to the previous branch, and gives off sundry twigs as follows:

(a) From its mesial side, one or two motor twigs to the *M. levator bulbi*.

(b) About three lateral branches which pass successively to the skin of the upper jaw as far as the anterior angle of the orbit.

Hoffmann describes an anastomosis between the latter branch and the *R. palatinus* VII, but no sign of such a fusion has been found—a result which is in harmony with the findings of Kingsley (1896). Hoffmann also suggests that the superior palpebral branch (his *R. dorsalis*) is the representative of the Selachian ophthalmicus superficialis. While it may possibly represent a portion of this nerve, it should nevertheless be noted that it emerges from the antrum

petrosum laterale by a different opening from the ophthalmicus profundus, and is separated from it by the processus ascendens of the quadrate.

The homologous comparison of the ophthalmicus profundus and maxillaris nerves of Urodeles with those of Selachians and Anura is not very easy. On the whole it seems most likely that Coghill's explanation is correct, and that the Urodele ophthalmicus profundus contains at least a considerable proportion of the fibres forming the Anuran maxillaris, thus accounting for the apparent difference in the trigemino-palatine anastomosis in these two groups. The Urodele maxillaris would then be the equivalent of Strong's 'accessory ramus' of the Anuran tadpole. This hypothesis also explains the size and complexity of the Urodelan profundus nerve, and the smallness of the maxillaris.

V₃. *R. mandibularis* (n.5c.) (mixed, general cutaneous, and visceral motor).

R. mandibularis (partim) von Plessen and Rabinowicz.
R. maxillaris inferior Hoffmann.

The remaining trigeminal branch leaves the antrum petrosum laterale by the same opening as the *R. maxillaris*—i.e. between the ascending and otic processes of the quadrate, and immediately turns ventrally towards the lower jaw. It is flat and ribbon-like in shape as it passes through the levator mandibulae muscle.

(i) Its first branch is a fine twig which turns mesially and dorsally, and innervates the *M. levator mandibulae anterior*—both superficial and deep portions. This branch leaves the nerve either just before or just after it emerges from the antrum petrosum laterale. The *MM. levator mandibulae posterior* and *externus* receive several very fine twigs from the main nerve as it passes ventralwards through them on its way to the lower jaw.

On reaching the mandible, just anterior to its articulation with the suspensorium, the nerve divides into two branches:—

(ii) A *cutaneous branch* (cut.) which turns posteriorly and supplies the skin overlying the angle of the jaw. From this branch is given off an *external mandibular nerve*—a very fine twig running parallel with the lower jaw and supplying the skin overlying the posterior two-thirds of the mandible.

(iii) The other main branch is a mixed nerve, and turns antero-ventrally, passing right through the mandible between the dentary and Meckel's cartilage. Within the jaw it gives off:

(a) An *internal mandibular, or inferior dental nerve* (n.m.i.) which

passes anteriorly in the alveolar canal of the lower jaw, latero-dorsal to Meckel's cartilage. It gives fine twigs to the teeth, while its terminal branches pass out laterally through foramina in the dentary to supply the skin covering the anterior part of the lower jaw, and may thus be called *RR. mentales*. It is important to notice that this branch throughout the whole of its course remains *lateral* to the primitive jaw. Stadtmüller (1924) describes a rather complicated anastomosing system between it and the R. alveolaris VII, which, however, is only traceable by means of sections.

(b) The main branch (n.m.c.) which passes right through the jaw and then turns anteriorly along its ventral side. It is a mixed nerve and supplies cutaneous branches to the skin between the rami of the mandible, and motor branches to the M. intermandibularis, while very occasionally its most posterior twigs may encroach on the region belonging to the VIIth nerve and enter the most anterior portion of the M. interhyoideus (cf. Drüner, 1901, p. 542). From its distribution it is known as *R. intermandibularis*.

VII. N. Facialis (n.7) (mixed, communis, visceral motor). In the Salamander the facial nerve leaves the brain in company with the auditory nerve and shares a common ganglion—the *acustico-facialis ganglion* (g. 7+8)—with it. The combined nerve leaves the lateral border of the medulla about $\frac{3}{4}$ mm. posterior to the trigeminus, and passes into a recess in the petrosal bone near the anterior end of the otic capsule, and ventral to the auditory organ. Within this recess the ganglion is situated. The fine R. communicans passing to the Gasserian ganglion has already been mentioned (p. 139). In the larva, where it is much larger, it arises independently from the medulla—according to Drüner—but in the adult it appears to leave the combined acustico-facialis nerve, or the ganglion itself. It is not always demonstrable.

The facial nerve separates from the ganglion and passes directly outwards through a canal in the petrosal bone—the *facialis canal*—beneath the auditory organ, and finally enters the antrum petrosum laterale (cf. p. 26).

(i) *R. Palatinus* (n.pal.) (communis). The palatine nerve is given off immediately distal to the ganglion, while the nerve is still in the facialis canal, and passes obliquely antero-ventrally through a special foramen in the floor of the petrosal bone (fo.pal. fig. 2), emerging from the foramen just lateral to the origin of the M. retractor bulbi. The nerve then turns antero-mesially and crosses the M. retractor bulbi, passing between the muscle and the epithelium of the roof of the mouth. At the postero-mesial

angle of the orbit it turns sharply anteriorly, passing alongside the tooth-bearing, backward extension of the pre-vomer. At a point a little anterior to the level of the optic nerve the palatine nerve passes dorsal to the pre-vomer, between it and the parasphenoid, and runs in a groove on the dorsal side of the former bone.

At this point, or a little posterior to it, a small twig may remain outside the groove to pass forwards lateral to the palato-nasal artery. This is the *lateral palatine nerve* (n.pal'.; Fig. 57). This nerve has not always been found, and in any case it is very fine. Nevertheless even its occasional presence is of interest in view of the condition in Siren, where it normally occurs and fuses with a special branch from the trigeminus nerve (cf. H. W. Norris, 1913). In the Salamander it enters the nasal capsule and fuses with a branch coming from the main palatine-profundus anastomosis to form the *post choanal nerve* (n.p.ch.) (see below). Besides this branch the main palatine nerve gives numerous fine fibres to the mucous epithelium of the palate, which frequently have the appearance of an anastomosing network, and are particularly conspicuous around the palato-nasal artery.

The main palatine nerve continues along the dorsal side of the pre-vomer, passing between it and the 'Planum internasale', and enters the nasal capsule through the fenestra basalis. Here it is immediately joined by the ventral terminal branch of the ophthalmicus profundus V at the mesial border of the internal narial opening. At the junction of these two nerves a fairly conspicuous ganglion occurs. A number of fine twigs are given off by the combined nerve, most of which pass anteriorly mesial to the internal narial opening, and spread over the roof of the mouth ventral to the olfactory epithelium, and ventral to the branches of the olfactory nerve. One branch, however, is given off laterally and passes round the posterior border of the internal nares where it is joined by the lateral palatine nerve—when such is present—to form the *post choanal nerve* (n.p.ch.).

No post-palatine nerve, such as occurs in some Urodeles, has been found in the Salamander, and therefore there is no Jacobson's anastomosis. This result is in agreement with those of previous workers (cf. also Coghill's paper on *Amblystoma*).

The remainder of the facial nerve, which may now be called the *truncus hyomandibularis* (n.hy.m.), on entering the antrum petrosus laterale turns posteriorly and leaves the antrum by its posterior opening, i.e. between the otic and basal processes of the quadrate. Immediately after emerging from the antrum it gives off, antero-mesially:

R. alveolaris (r.al.) (communis)

R. mandibularis internus Hoffmann.

At the point where this branch is given off, von Plessen and Rabinowicz, Hoffmann and Drüner report a few scattered clusters of ganglion cells, but they are only detectable by microscopic means. Von Plessen and Rabinowicz call them the buccal ganglion. Drüner is convinced that they do not represent the remains of the ganglion laterale VII (connected with the lateral line system), and also finds fine sympathetic fibres entering the nerve in this region. Hoffmann goes further and suggests that the ganglion may be the forerunner of the otic ganglion of mammals. Certain it is that it exists and that it has a connexion with the sympathetic system.

The alveolar nerve turns a little antero-laterally, and, keeping ventral to the quadrate and pterygoid, passes to the mesial side of the lower jaw. At about the level of the processus coronoideus it penetrates a foramen in the pre-articular (fo.i.den; Fig. 7) and comes to lie between this bone and Meckel's cartilage—that is, on the *mesial* side of the latter. The nerve then passes anteriorly through the alveolar canal and emerges from it, anterior to the pre-articular, between the edges of the dentary. Its ultimate branches are distributed to the epithelium of the mouth-floor, between the M. genio-glossus and the mandible. Within the jaw it anastomoses several times with the internal mandibular branch of the Vth nerve as above noticed, but as a whole these two nerves are separated from one another by Meckel's cartilage.

Homology of Chorda tympani.

A very great deal has been written on, and around, this subject, and the conclusions drawn therefrom have been widely different. Only the briefest résumé of the discussion may be given here.

The chorda tympani is typically a mammalian nerve, and receives its name from its relations in the human subject, where it appears to pass through the middle ear, or tympanum, across the dorsal edge of the tympanic membrane. Actually the nerve is outside the tympanum altogether, morphologically speaking, since it is covered by the mucous lining of the cavity. After receiving fibres from the otic ganglion it joins the lingual nerve—a branch of the Vth nerve—and with it enters the inferior dental canal of the lower jaw.

Now the chorda tympani is a branch of the facial nerve, which in turn is a visceral nerve related to the spiracle or its homologue. Hence the question arises whether, if a nerve corresponding to the

chorda tympani occurs in lower vertebrates at all, it is to be looked for as a branch of the pre- or post-trematic nerve. In 1881 Balfour claimed that it was a *pre*-trematic branch of the VIIth nerve. In 1887 Froriep came to the conclusion that the chorda tympani is to be regarded as a *post*-trematic nerve, and although others have since supported Balfour's alternative suggestion, Froriep's conclusion represents the view now generally held.

This discussion with regard to the morphological position of the chorda tympani has considerably complicated the second point at issue, namely, whether the R. alveolaris VII of the Salamander, and other Urodeles, is pre- or post-trematic, and is therefore to be regarded as the true homologue of the chorda tympani or not.

In 1895 Strong came to the conclusion that the chorda tympani of mammals, the R. mandibularis internus VII of Anura, and the R. alveolaris VII of Urodeles were all homologous structures.

In 1901 Drüner, who apparently accepted Froriep's view that the chorda tympani is post-trematic, denied its homology with the R. alveolaris VII of Salamandra on the ground that he believed the latter nerve to be pre-trematic. In both larval and adult Salamander the floor of the mouth is somewhat depressed ventrally between the mandibular and hyoid arch so as to form a sort of pocket—the plica hyomandibularis (plc.hy.m.; Figs. 37 and 38)—and this has been supposed to represent a vestige of the gill-slit between these two arches. On this supposition therefore Drüner argued that, since the R. alveolaris VII is a sensory branch of the hyomandibular nerve lying anterior to this supposed hyoid cleft, it must be pre-trematic. He accordingly thought the homologue of the chorda tympani was wanting in Urodeles.

In 1902 Coghill, while accepting the view that R. alveolaris VII is a pre-trematic nerve, apparently regarded the chorda tympani also as a pre-trematic nerve, and, maintaining at the same time a somewhat cautious attitude, held them to be homologous. He could not, however, agree with Strong in regarding these two structures as homologous with the R. mandibularis internus of Anura, since he believed this nerve to be post-trematic.

In the same year C. K. Hoffmann (1902) regarded both the chorda tympani and the R. alveolaris VII of Salamandra as pre-trematic branches of the VIIth nerve, and held that they were homologous structures.

By 1903 Drüner's views had undergone a profound change. As the result of the investigation of a developmental series of Siredon he found that the R. alveolaris VII was morphologically post-trematic

and developed posterior to the rudiment of the hyomandibular cleft, while the plica hyomandibularis was a secondary structure, developing behind the R. alveolaris VII, and in no way related to the visceral cleft. The true R. pre-trematicus VII he identified with a small branch of the R. palatinus VII distributed to the quadrate. In his later paper, 1904, he confirmed these results.

Thus the matter stands, and the accepted views with regard to the questions enunciated above may be summarized.

(i) The chorda tympani is a post-trematic branch of the VIIth nerve.

(ii) The R. alveolaris VII of Urodeles is the true homologue of the chorda tympani of Mammals.

It should be noted that the above résumé is confined to the more immediately relevant literature and that all reference to the more general, but nevertheless important papers by Cole, Goodrich, Herrick, and Ruge, has been omitted for the sake of brevity.

Very close to the point from which the R. alveolaris separates, the R. *communicans* IX+X ad VII (r.9+10-7) joins the main nerve.¹ Drüner claims that it brings motor-fibres from the IXth nerve which join those of the R. jugularis VII. This is almost certainly incorrect. Without direct observation it is unsafe to make a definite statement, but it seems very probable that the condition in the Salamander resembles that described by Coghill for Amblystoma, viz. that the Xth nerve sends *general cutaneous* fibres which enter the R. jugularis VII, while the IXth nerve contributes *communis* fibres to the R. alveolaris VII. One feature which strongly supports this assumption is that one not infrequently finds the R. *communicans* bifurcating just before reaching the VIIth nerve, and one portion, the smaller, passing towards the R. alveolaris, and the other entering the R. jugularis about a millimetre further distalwards. It should, however, be noted that the same author can find no glossopharyngeal fibres in the R. *communicans* of Triton but only general cutaneous fibres from the vagus.

After the separation of the R. alveolaris from the Truncus hyomandibularis the remainder of the nerve becomes known as:

R. *jugularis* (n.j.) (visceral motor, and general cutaneous derived from vagus).

R. mandibularis externus Hoffmann.

Its first branch, (*a*), arises very close indeed to the point where the R. *communicans* IX+X ad VII enters it, and in fact it usually

¹ The R. *communicans* may be easily displayed by dissecting the M. depressor mandibulae away from its origin on the squamosal and turning it over ventrally.

appears to spring from the angle formed by these two nerves. It is a *R. muscularis* to the *M. depressor mandibulae*.

The main nerve continues ventro-laterally, passing between the above-named muscle and the squamosal to the surface of the muscle. Here it turns posteriorly, passing right across the muscle, between it and the skin. In doing so it gives off (*b*) one or two *RR. cutanei* to the overlying skin.

At the posterior border of the *M. depressor mandibulae* the nerve makes yet another half-turn, and pursues an antero-mesial course, passing dorsal to the *M. interhyoideus posterior*, and ventral to the *M. interhyoideus*. A few fibres enter the *M. interhyoideus posterior* from its dorsal surface, while others turn back over its anterior edge and enter the muscle from the ventral side (*i.hy.p.*). The larger part of the nerve, however, spreads out fan-wise over the *M. interhyoideus* and innervates it (*i.hy.*). A few of the more lateral twigs pass right across the muscle to the space between it and the *M. intermandibularis*, and then turn dorsalwards to supply the *M. subhyoideus*, while a few fine fibres may pass right through the *M. interhyoideus* and enter the *M. subhyoideus*.

Drüner (1901) thinks that the glossopharyngeal nerve also contributes motor-fibres to these muscles by means of the *R. communicans*, but, as stated above, it is exceedingly unlikely that the Salamander is so different from all other Urodeles, which have been investigated from the point of view of nerve components, as to possess motor-fibres in the *R. communicans IX+X ad VII*.

Besides the motor branches to the interhyoid muscles described above there also arise, from the same fan-like termination of the nerve—the *Pes anserinus* (Drüner)—a number of sensory branches, which are (*c*) *RR. cutanei intermandibulares* (Drüner), supplying the skin underlying the muscles.

Finally a few of the most anterior fibres of the *R. jugularis* may very occasionally extend to the trigeminus region and enter the posterior edge of the *M. intermandibularis*.

VIII. N. Acusticus (*n.8*). As above described the auditory nerve is indistinguishable from the facial nerve until it separates from the acustico-facialis ganglion. It leaves this ganglion posteriorly, and enters the auditory sac by three foramina at the base of its mesial wall. The three foramina correspond to the three divisions of the auditory nerve.

(i) The *R. anterior* (*n.8.a.*) supplies the recessus utriculi and the ampullae of the anterior and horizontal canals.

(ii) The *R. medianus* (*n.8.m.*) is a very fine nerve and supplies only the sacculus.

(iii) The *R. posterior* (n.8.p.) gives twigs to the ampulla of the posterior semicircular canal, to the lagena, and to the macula acustica neglecta.

The *R. medianus* and its corresponding foramen were first described for Salamandra by Okajima in 1910, and its existence was confirmed in other Urodeles and in Anura by Miyawaki (1927-9).

IX and X. NN. Glossopharyngeus and Vagus.

The roots and ganglia of these two nerves are very closely associated in the adult Salamander, although—according to Hoffmann—they are distinct in the larva. It is therefore convenient to regard them as forming a complex arising laterally from the sides of the medulla oblongata by three roots, which unite and pass out of the cranial cavity through the *foramen post-oticum* (for. metoticum, Stadtmüller), immediately posterior to the ear-capsule. The composite nerve then swells into a large *glossopharyngeus-vagus ganglion* which is thus situated outside the skull, in the angle between the ear-capsule and the occipital segment, and at about the level of the dorsal surface of the former. To expose it the MM. depressor mandibulae, cephalo-dorso-subpharyngeus, cucullaris, and intertransversarius capitis superior must be removed, or turned back.

IX. N. Glossopharyngeus (n.9) (mixed communis, visceral motor, and a few general cutaneous fibres). The glossopharyngeal nerve separates from the anterior portion of the ganglion and passes lateralwards between the MM. intertransversarius capitis superior and inferior, and then turns ventrad, lateral to the M. opercularis and mesial to the M. cucullaris. As it proceeds it gives off three branches.

(i) *R. communicans ad VII* (see p. 148) separates at about the level of the operculum and passes anteriorly round the otic capsule to join the facial nerve as described above. This branch probably carries only communis fibres from the glossopharyngeus and derives a general cutaneous component from the vagus.

(ii) *R. pre-trematicus* (n.pr.t.9) (communis). This branch is given off very soon after the former, and at first passes anteriorly at right angles to the main nerve, but just posterior to the *R. jugularis VII* it turns ventrad and runs parallel with the internal carotid artery, and anterior to it. The *R. pharyngeus* (n.phar.) which, arising at the point where it turns ventrad, passes mesially, just anterior to the systemic arch, and is distributed to the mucous epithelium of the pharynx roof. Drüner describes ganglion cells associated with this

nerve as well as connexions between it and the sympathetic system. It is associated with the pharyngeal branches of the succeeding nerves in the formation of a pharyngeal plexus. All these nerves are exceedingly fine and very difficult to dissect.

The main portion of the R. pre-trematicus IX is distributed to the epithelium of the mouth-floor directly dorsal to the cerato-hyal cartilage.

(iii) *R. post-trematicu* (n.po.t.9) (general cutaneous, visceral motor, and communis). After the R. pre-trematicus has been given off, the post-trematic branch—constituting the major portion of the nerve—passes ventrally, parallel with the internal carotid artery, to the dorsal end of the posterior cornu (cerato-branchial I) of the hyo-branchial apparatus. Just before leaving the artery it gives off:—

(a) One or two *RR. cutanei jugulares* (n.cut.j.) (Drüner) which pass to the skin overlying that region. They are exceedingly fine.

(b) *RR. pharyngei dorsales* (Drüner), also very fine nerves distributed to the dorsal wall of the pharynx and, according to Drüner, associated with sympathetic fibres around the internal carotid artery.

In its course from the arterial arch to the cerato-branchial cartilage the nerve passes round the dorsal side of the large jugular lymph sinus, thus producing a loose loop which allows for the stretching of the nerve on the extrusion of the tongue. It then passes along the dorso-mesial side of the third visceral arch to the copula, giving off numerous twigs.

(c) *RR. musculares*, to the M. subarcualis rectus I. The remainder of the nerve now becomes:

(d) *R. lingualis*, and passes between the radials of the copula where it swells into a small ganglion—*Ganglion copulare* (Drüner)—from which emerge two or more branches passing directly into, and ramifying through the tongue. The nerve is the sensory nerve to the tongue.

Belonging perhaps to both IXth and Xth nerves are the *NN. Cutanei occipitales, anterior and posterior* (nn.cut.oc.) (Drüner) arising from the dorsal side of the IX+X ganglion. These nerves, carrying general cutaneous components, pass through the overlying muscles—usually somewhat lateral to the M. intertransversarius capitis superior—to the skin covering the occipital region. In the larva they are associated with a lateralis component which atrophies during metamorphosis.

X. N. Vagus+Accessorius Willisii (mixed communis, visceral motor, general cutaneous fibres). The Xth nerve of *Salamandra* is an

interesting example of the transition from a primitive fish-like state towards the condition found in more specialized land vertebrates. For example, the fourth and fifth visceral arch nerves retain a considerable amount of independence, and remain definitely associated with their respective arteries, while the nerve belonging to the sixth visceral arch has become more specialized, although still easily recognizable, and travels for a considerable distance in the track of the intestinal trunk. A careful study of Pl. X, fig. 54 will make this clearer.

(1) *Fourth visceral arch nerve* (n.vis.4).

2nd Gill-arch nerve Drüner.

Nearly always this nerve leaves the ganglion together with the fifth visceral arch nerve, but occasionally they remain quite distinct from the start. It passes lateral to the M. opercularis, and mesial to the M. cucullaris, as do the other visceral nerves emerging from the glossopharyngeus-vagus ganglion. Its course round the oesophagus lies between the carotid and systemic arches. About 4 mm. distal to the ganglion it gives off:

(a) *R. pharyngeus* (n.phar.) which passes back mesially over the roof of the pharynx to enter the pharyngeal complex mentioned above.

(b) *RR. cutanei jugulares* (n.cut.j.) which are given off at about the level of the carotid gland. They correspond with those already described for the glossopharyngeal nerve.

A short distance beyond this point the nerve divides into two terminal branches (c) and (d).

(c) *R. muscularis* for the M. subarcualis rectus I (s.r.1) passes ventral to the common carotid, then, turning lateralwards, enters the muscle at the posterior end. It usually unites with a corresponding branch from the R. recurrens intestinalis X, and sometimes with one from the fifth visceral arch nerve also. According to Drüner this muscular branch may be missing, but no such case has been met with by the present author. The nerve between the arterial arches and the muscle is greatly convoluted, thus allowing for the free movement of the hyobranchial apparatus.

(d) *R. recurrens* (n.rec.4). This is a sensory branch and passes dorsal to the common carotid. It ramifies over the middle region of the mouth-floor, to the mucous epithelium of which its fibres are distributed. Drüner reports occasional ganglion cells along its course.

The same author considers that the whole visceral nerve as de-

scribed above is to be regarded as the R. post-trematicus only, since he finds in the larva an exceedingly small R. pre-trematicus, only distinguishable as such by its position relative to the gill-slit, so that, even supposing that the nerve persists after metamorphosis—which is doubtful—it is quite unrecognizable after the gill-slit has disappeared.

(2) *Fifth visceral arch nerve* (n.vis.5).

3rd Gill-arch nerve Drüner.

This nerve is very similar to the one just described and, as already mentioned, it is usually combined with it for a greater or lesser distance from the ganglion outwards. It passes round the oesophagus between the systemic and the 'third' arterial arches, and represents only the post-trematic branch. It is almost certain that the pre-trematic branch is wanting in the adult. Soon after leaving the ganglion it gives the following five branches.

(a) *R. muscularis* for the M. cephalo-dorso-subpharyngeus (c.ph.). This branch leaves the nerve posteriorly and enters the muscle from its mesial side.

(b) *RR. pharyngei*, corresponding to those of the previous nerve, come off very soon after, as do also:

(c) *RR. cutanei jugulares* to the overlying skin.

The remainder of the nerve may now divide, as did the previous one, into:—

(d) *R. muscularis*, passing ventral to the systemic arch to join the corresponding branch of the fourth visceral nerve and supply the M. subarcualis rectus I,

(e) *R. recurrens* (n.rec.5) passing dorsal to the aortae and distributed to the floor of the pharynx. More usually, however, the former branch is missing.

(3) *Truncus intestino-accessorius* (Drüner). The main branch of the Xth nerve (n.tr.int.acc.) leaves the ganglion more posteriorly than the two branches already described and passes in an oblique postero-ventral direction, lateral to the M. opercularis, and mesial to the MM. cephalo-dorso-subpharyngeus, dilatator laryngis, and cucullaris.

Very soon after leaving the ganglion the nerve gives off three branches:

(a) A *R. muscularis* anteriorly, which supplies the dorsal part of the M. cephalo-dorso-subpharyngeus, and then posteriorly:

(b) The *R. accessorius* (n.acc.) to the *M. cucullaris*. This nerve enters the muscle on its mesial side. It is a fairly large branch.

(c) The *RR. pharyngei* are very fine twigs to the pharynx corresponding with those already described for the other visceral nerves.

Drüner (Tafel 29, fig. 37) figures two fine twigs leaving the nerve at about this point and entering the *M. levator scapulae* (opercularis). In spite of very careful searching these twigs have not been found, and one can only suppose that, if they are of normal occurrence, they must be exceedingly fine. He does not mention them in the text.

(d) Almost immediately afterwards one or two *RR. musculares* (d.l.) for the *M. dilatator laryngis* are given off. They are very fine and are best seen by lifting the muscle carefully from its dorsal origin, when they will be seen stretching across through the connective tissue on its mesial side. Unless they are found in this way before the muscle is removed it is almost impossible to pick them up afterwards.

At the ventral edge of the *M. opercularis* a very fine anastomosis with the hypoglossal nerve can sometimes be found, and almost immediately afterwards is given off:

(e) The *R. recurrens* (n.rec.10). This important branch passes mesialwards, ventral to the *V. facialis*, and proceeds to divide as follows:—

(i) *N. laryngeus ventralis* (n.lar.v.).

R. laryngeus Drüner.

This nerve comes off variously, either soon after the *R. recurrens* separates from the intestinal branch, or later as the former nerve turns oralwards (i.e. as Drüner describes). In the former case it is combined with the ramus muscularis for the *M. dilatator laryngis*. It passes directly mesiad, ventral to the muscles, and enters the *M. constrictor laryngis* ventrally.

(ii) *R. muscularis* (d.l.) for the *M. dilatator laryngis*. This twig arises soon after the separation of the recurrent branch, either separately, or together with the former branch. It turns posteriorly and enters the muscle on its ventral side.

(iii) *RR. musculares* for the *M. cephalo-dorso-subpharyngeus*, comprising a number of fine twigs entering the muscle from the ventral side.

(iv) Amongst the former twigs a fine branch leaves the main nerve and passes along the ventral side of the *M. cephalo-dorso-subpharyngeus* to enter the *M. transversus ventralis IV*.

(v) *A sensory branch* to the mucous epithelium of the pharynx and mouth leaves the recurrent nerve close to the foregoing branches on the ventral side of the M. cephalo-dorso-subpharyngeus. It passes dorsalwards to the floor of the pharynx between the pulmonary arch and the above-named muscle. It is relatively of fair size, and corresponds with the recurrent branch of the fourth and fifth visceral nerves and, like them, passes *dorsal* to the arterial arches.

The remainder of the nerve then turns anteriorly and remains *ventral* to the arterial arches. It passes very close to the truncus arteriosus, and, at about the level of the pulmonary arch, it gives off:

(vi) A fine *anterior cardiac nerve* (n.c.a.) to the truncus arteriosus. The residue of the nerve is now:

(vii) The *R. muscularis* for the M. subarcualis rectus I. It passes anteriorly and fuses with the corresponding branch of the fourth visceral nerve, and with that of the fifth visceral nerve also—when such is present.

Drüner reports that a large number of ganglion cells are to be found in the region of the R. recurrens, both ventral to the muscles and on the branches to the mucous epithelium.

These various branches of the recurrent nerve are somewhat difficult to dissect owing to their small size and rather pale colour. The dissection is best carried out from a ventro-lateral aspect. The cucularis muscle must be removed and the M. rectus cervicis pulled over ventrally, and then the nerves may be detached from the connective tissue in which they are embedded.

(f) From the intestinal trunk immediately posterior to the recurrent nerve is given off to the larynx a fine branch which is here named *dorsal laryngeal nerve* (n.lar.d.). It appears to have been overlooked by Drüner since he does not mention it in his paper. Its position relative to the M. dilatator laryngis appears to vary somewhat, since it has been found both anterior and posterior to the muscle. In either case, however, it passes mesially, closely applied to the wall of the pharynx, and *dorsal* to the laryngeal artery. Although it appears to terminate in the M. constrictor laryngis and sends a branch to the dilatator muscle, its translucent appearance and close relation to the pharyngeal wall would lead one to suspect that it is probably in the main a sensory nerve to the larynx.

The intestinal nerve divides into pulmonary and gastric branches almost immediately after giving off the branch just described.

(g) The *common pulmonary nerve* (n.pul.) is the more ventral of the two and soon divides again into two.

(i) A *lateral pulmonary nerve* (n.pul.l.), which accompanies the

pulmonary artery down the side of the lung and ramifies over its surface with the arterial branches.

(ii) The *anterior pulmonary nerve* (n.pul.a.) passes mesially and ramifies over the anterior end of the lung and the muscle-fibres of that region. It passes to the point where the pulmonary vein leaves the lung on the mesial side, and there gives off two branches.

(a) One or more *posterior cardiac nerves* (n.c.p.) which accompany the pulmonary vein to the heart.

(b) The *gastric nerve* (n.gas.) which proceeds posteriorly for some distance, lateral to the lung, and then turns mesially and divides into two.

(i) A *ventral gastric branch* (n.g.v.) distributed to the ventro-lateral stomach wall, and

(ii) A *dorsal gastric branch* (n.g.d.) supplying the dorso-lateral wall.

SPINO-OCCIPITAL NERVES (Pl. X, fig. 54, n.sp.occ.)

Drüner (Teil 1, p. 553 et seq.) describes a fine anastomosis leaving the ventral side of the glossopharyngeal vagus ganglion and passing round the occipital condyles laterally to join the ventral ramus of the first spinal nerve. He considers it is probably the homologue of the spino-occipital nerves of Selachians and Holocephali described by Fürbringer (1896).

His results have been confirmed for *Salamandra* (n.sp.occ.) and a nerve has been found leaving the IX+X ganglion close to the branch just described which fuses with the dorsal ramus of the N. spin. 1, within the M. intertransversarius capitis superior (n.sp.occ'). Drüner mentions this connexion as a rare occurrence. It is very fine and difficult to dissect so that it is easily missed.

These nerves may represent the ventral roots belonging to segments which have become fused together in the occipital region of the skull posterior to the vagus, but Drüner was not able to satisfy himself entirely on this point as he could not trace their centres of origin in the medulla. In this connexion reference should be made to the more recent work of Goodrich (1911) and of de Beer (1926) on the segmentation of the vertebrate skull in general.

SPINAL NERVES

1. Historical.

Most authors who have described the cranial nerves, e.g. Fischer, von Plessen and Rabinowicz, Drüner, and Hoffmann, have included the first spinal nerve in their account, since it supplies certain muscles connected with the hyobranchial apparatus and tongue. Details of the discussion relating to the morpholo-

gical position of this nerve advanced by these and other authors are given below.

The brachial plexus was well described by Fürbringer in 1873, and his account was republished five years later by Hoffmann in Bronn's *Thier-reich*. In this latter work Hoffmann also published an account, accompanied by an original figure of the crural plexus. His description is not quite complete.

A number of authors have dealt with various details connected with the nerves of the limbs in papers primarily concerned with muscles, which are summarized in the muscle-section of the present work. Amongst these may be mentioned Sieglbauer, Ribbing, Appleton, and McMurrich.

Amongst the synonyms given will be found the names of authors dealing with Urodeles other than Salamandra, which have been included to facilitate comparison.

The method adopted here is the same as that chosen by Gaupp in his *Anatomie des Frosches*, viz. to describe first a typical spinal nerve—for which purpose N. spinalis 10 has been chosen—and then to give an account of the ventral rami of those nerves which become specially modified, e.g. N. hypoglossus, and the nerves supplying the fore- and hind-limbs.

2. A Typical Spinal Nerve.

N. spinalis 10 (Pl. XXIV, fig. 79) arises from the spinal cord by a dorsal and a ventral root. The dorsal root arises some distance posterior to the ventral root, but both pass together through a special foramen in the neural arch immediately posterior to the transverse process of the ninth vertebra (see also p. 19). The two roots fuse within the foramen, and immediately after emerging from it swell into a large ganglion—the spinal ganglion 10 (g.sp.10). The spinal ganglion thus lies outside the vertebral column, but it is nevertheless protected by the transverse process anteriorly, and by the broad articular processes dorsally, as well as by the tough fibrous sac in which it is enclosed. Within this sac, surrounding the ganglion, is a spongy fatty tissue, and there is no trace of the chalky masses found in this position in the frog.

From the ganglion emerge the usual dorsal and ventral rami, each being composed of motor and sensory fibres, and supplying respectively the dorsal and ventral body muscles and the skin overlying them.

R. dorsalis. This ramus arises from the ganglion as several twigs. The largest of these emerges dorsally, then turning directly caudad, passes alongside the vertebral column almost to the level

of the next transverse process. Here it turns sharply dorsally again and passes between the MM. interspinales and dorsalis trunci to supply the skin of the back. During its course parallel with the vertebra it gives off one or two twigs to the above-named muscles. This nerve would appear to correspond with the *R. cutaneus dorsi medialis* (n.cut.d.m.) of Gaupp (Frog), carrying with it some motor-fibres.

Another cutaneous branch, rather smaller than the previous one, and evidently representing the *R. cutaneus dorsi lateralis* (n.cut.d.l.) of Gaupp (Frog), emerges from the lateral aspect of the ganglion. Then, passing towards the transverse process, it penetrates the tough connective tissue surrounding the bone and myosepta of the M. dorsalis trunci, and supplies the overlying skin. There are also two small muscular branches leaving the lateral aspect of the ganglion, one turning dorsally into the main portion of the M. dors. trunci, and the other passing into the intertransversarius portion of the same muscle.

R. ventralis. This ramus is considerably larger than the ramus dorsalis and forms the main portion of the nerve. It leaves the ventro-lateral aspect of the ganglion, and, as its name implies, is distributed to the muscles and skin of the ventral body-wall. It passes for a short distance through the sub-vertebral muscles and supplies them with fibres, then immediately after, or just before emerging from them ventrally, it gives off the *R. communicans ad sympathicus*. The nerve then passes around the body-wall between the peritoneum and the muscles, giving off a cutaneous branch about midway—the *R. cutaneus abdominis lateralis* (n.cut.ab.l.). It then supplies several twigs to the MM. obliquus externus superficialis and profundus, and to the ventral portion of the M. transversarius s. obliquus internus.

At the lateral edge of the M. rectus abdominis profundus it sends a branch to the muscle (r.ab."), and then divides into muscular and cutaneous branches. The former (r.ab.') passes deep to the muscle and supplies the M. rectus abdominis superior, while the latter becomes superficial and supplies the skin over the belly—*R. cutaneus abdominis medialis* (n.cut.ab.m.).

The exceptions to the general plan exemplified by the tenth spinal nerve described above will now be considered individually and in detail. They may be summarized briefly:

The first spinal nerve has no dorsal root and only exceptionally a ganglion in the adult. There is no dorsal cutaneous branch and the ventral ramus supplies the tongue muscles.

The second spinal nerve is normal with regard to its dorsal root, ganglion, and cutaneous branches, but its ventral ramus contributes both to the N. hypoglossus—supplying the tongue muscles—and to the brachial plexus.

The third, fourth, and fifth spinal nerves are all exceptional in that their ventral rami enter into the brachial plexus and supply the muscles of the fore-limb and shoulder.

The ventral rami of the fifteenth, sixteenth, and seventeenth spinal nerves similarly anastomose to form the crural plexus supplying the muscles of the pelvis and hind-limb. To this plexus the fourteenth and eighteenth spinal nerves also contribute, but only in a minor degree.

3. The First Spinal Nerve.

N. spinalis 1 (= *N. spinalis 2*, Hoffmann) (Pl. X, fig. 54, n.sp.1). There has been some controversy over the morphological position of this nerve, together with the related question of the segmentation of the occipital region of the skull and of the 'atlas' vertebra (see also p. 17).

So far as it is possible to separate the discussions concerning the nerve itself from those relating to the skeletal structures they may be briefly stated as follows.

In 1878 Hoffmann suggested that the first vertebra of Urodeles actually represents two vertebrae fused because it is penetrated by the first spinal nerve. In 1902 he confirmed this view by studying the larval stages of Triton and Salamandra. He then found the ventral root of a transitory nerve emerging between the occipital condyles and the vertebral column—*N. suboccipitalis*—and related to the first myotome. He regarded this transitory nerve as the first spinal nerve because it emerges between the occiput and the vertebral column, and therefore he argued that the first spinal nerve of the adult is morphologically *N. spinalis 2*. He also found an even more transitory nerve (ventral root only) anterior to the *N. suboccipitalis* belonging to his myotome-o.

Drüner (1904) disagreed with this view. He accepted Peter's explanation that the atlas vertebra was single and not two vertebrae fused, and said (Teil II, p. 439, footnote): 'Nach meinen Befunden ist der den 1. Wirbel durchsetzende Nerv mit demjenigen identisch, welchen C. K. Hoffmann bei jüngern Embryonen zwischen Occipitalknorpel und 1. Wirbelbogen austreten sah.'

Goodrich (1911) apparently arrived at similar results from the study of the larva of Amblystoma.

In 1917 Froriep, as the result of studying the larval stages of *Salamandra atra*, returned to Hoffmann's view. He found a sub-occipital nerve which he regarded as the first spinal nerve, and came to the conclusion that the atlas vertebra is a double one and therefore that the first spinal nerve of the adult is morphologically the second.

More recently, Mookerjee (1930) has shown that in Triton the atlas, although it has a double origin, is not strictly a double vertebra (cf. 'atlas' in skeletal section). He finds the sub-occipital nerve, however, and calls it N. spinalis 1, and calls the hypoglossal nerve, N. spinalis 2.

To summarize: it seems certain, therefore, that the rudiment of the nerve which appears between the occipital condyles and the vertebral column should be regarded as N. spinalis 1, and that the next posterior, which is the first spinal nerve of the adult, is morphologically N. spinalis 2. Nevertheless since the N. suboccipitalis is so very transient and probably never attains functional importance, it seems unnecessary to insist on using the strict morphological nomenclature, thereby confusing the description of all the remaining spinal nerves. In the following account the nerves are accordingly numbered as they appear in the adult, leaving the N. suboccipitalis out of the series.

The first spinal nerve arises from the spinal cord by two *ventral* roots only. A dorsal root and a ganglion occur in the larva, but they atrophy during metamorphosis. Drüner reports that in three out of fifteen adults he finds a trace of the ganglion remaining, but such a circumstance has not come under the notice of the present writer. Correlated with the absence of the ganglion there is no dorsal cutaneous branch, but the dorsal muscular branches are present and innervate the MM. intertransversarius capitis superior and inferior, and the M. rectus capitis posterior.

The *R. ventralis* passes directly ventral between the subvertebral and dorsal musculature, and immediately on reaching the ventral surface of the muscles it gives off (i) a very fine *ramus communicans ad sympathicus* (r.com.ad.sym.). It then turns somewhat posterolaterally and gives off two more branches.

(ii) A small twig to the M. intertransversarius capitis inferior (i.c.i.).

(iii) One or two twigs to the M. opercularis (o.) as it passes ventral to the edge of this muscle.

At this point the nerve passes very close to the tenth cranial nerve just at the point where the latter divides into gastric and pulmonary branches. A very fine anastomosis is usually discernible at the

juxtaposition of these two nerves, but it does not appear to be quite constant.

The first spinal nerve now turns anteriorly and in doing so passes between the subclavian vein and the small cutaneous vein.

(iv) Immediately ventral to the subclavian vein a strong *anastomosis* from the second spinal nerve is received, so that the vein passes through the angle between the anastomosis and the proximal portion of the main nerve. The nerve thus formed, containing fibres from the ventral branches of both first and second spinal nerves, is the *N. hypoglossus* proper.

(iv a) From the middle of the anastomosis a fine twig is given off to the *M. pectori-scapularis* (p.s.).

(v) *N. hypoglossus* (n.hyp.) (*N. hypobranchialis*, Drüner). Immediately after its formation, as the result of the fusion of branches from the first two spinal nerves, the hypoglossal nerve turns directly forwards along the lateral edge of the *M. rectus cervicis*. It supplies several twigs to both the superficial and deep portions of this muscle, then passes ventral to the thyroid gland, and at the anterior end of the gland turns somewhat mesially to pass through the substance of the *M. genio-hyoideus*. It supplies several fine twigs to this muscle (g.hy.) and emerges from it at the anterior end of the cerato-hyal (see Figs. 37 and 38) to enter the tongue and innervate the *MM. genio-glossus* and *hyo-glossus*.

With regard to the homology of the hypoglossus of Urodeles with that of the higher vertebrates the statement of Goodrich (*P.Z.S.* 1911, p. 118) may be quoted here. He says '... the hypoglossus of Amphibia and Amniota may certainly be considered as homologous, although not necessarily composed of the same segmental nerves. It is owing to the shortness of the skull in Amphibia that the hypoglossal roots come out behind it.' In the same paper he also shows that the urodele hypoglossus innervates muscles derived from the ventral outgrowths of the second, third, and fourth myotomes.

4. The Second Spinal Nerve.

N. spinalis 2 (Pl. XI, fig. 55, n.sp.2) possesses both dorsal and ventral roots and also a ganglion, so that its dorsal branches contain both cutaneous and motor-fibres, and hence conform to the normal plan.

The *R. ventralis*, after emerging from the subvertebral musculature, gives off the *R. communicans ad sympathicus* and turns posterolaterally to the anterior border of the shoulder. Here, according to Fürbringer, it divides into four main branches: (i) *N. thoracicus superior* 2; (ii) *N. thoracicus inferior* 2 anterior; (iii) *N. thoracicus*

inferior 2 posterior; and (iv) a branch to the ventral body muscles and the skin of the neck.

With the exception of the first branch this does not seem to give a very accurate picture of the branching of the nerve, which is much more variable than Fürbringer's figure and description suggest.

(i) *N. thoracicus superior* 2 comprises two or three fine branches which turn dorsalwards and supply, (a) the M. thoraci-scapularis (t.s.), and (b) the M. cucullaris minor (c') near its insertion.

(ii) Almost immediately after giving off this branch the nerve turns a little anteriorly and sends two fairly stout cutaneous branches which spread over the skin at the base of the neck region and over the procoracoid and the anterior edge of the scapula. After separating from the nerve they pass directly laterally and emerge at the angle between the procoracoid and the M. cucullaris. It is very difficult to be sure whether or not they supply any motor-fibres to the MM. procoraco-humeralis and cucullaris, but it is very probable that they do not. These nerves supply a region corresponding with that supplied by the supra-clavicular nerves of man, and as this name is hardly appropriate in an animal not possessing a clavicle, they are therefore called here *cutaneous cervical*, or *NN. cutanei cervicales* (n.cut.cer.).

(iii) After a very fine twig to the M. pectori-scapularis has been given off the nerve very soon divides, more or less equally into its three terminal branches, as follows:—

(iv) *R. communicans ad N. spinalis* 1, which has already been described—see above.

(v) A *R. muscularis* to the MM. rectus cervicis superior and profundus. The branch to the former muscle passes mesial to the profundus muscle.

(vi) A *R. communicans ad N. spinalis* 3 (r.com.2-3) which arises somewhat variously. It may consist of a single bundle, separating from the main nerve near the point where it turns anteriorly, close to the N. thoracicus superior 2, to join the third spinal nerve near the point where the N. supracoracoideus emerges. It bifurcates at this point, one branch entering the N. supracoracoideus direct, while the other crosses this nerve and enters the main trunk of N. spinalis 3. Quite frequently, however, an auxiliary bundle arises separately from the second spinal nerve, and passes obliquely to join the N. supracoracoideus just before it passes through the For. supracoracoideum in the pectoral girdle.

The series of anastomoses, Spino-occipital—N. spinalis 1; N. spinalis 1—N. spinalis 2; and N. spinalis 2—N. spinalis 3, is frequently spoken of as the *cervical plexus*.

5. Brachial Plexus, and Nerves of the Fore-limb (Pl. XI).

The actual plexus and the nerves supplying the flexor muscles of the limb are best dissected from the ventral side, but the nerves to the extensor muscles should be dissected dorsally.

The precise pattern of the plexus varies considerably, but the net result obtained is always the same, namely, that most of the fibres from N. spinalis 3 pass to the dorsal side of the limb and innervate the extensor muscles, while the major portion of N. spinalis 4 remains ventral and supplies the flexor muscles. N. spinalis 5 makes only a small contribution to the plexus, which mainly enters N. pectoralis.

Third spinal nerve (ventral branch) (n.sp.3).

Very soon after emerging from the subvertebral musculature the third spinal nerve gives off dorsally one or two fine branches to the M. thoraci-scapularis (= NN. thoracicus superior 3, Fürbringer). Shortly afterwards a small branch is given off mesially which divides to supply the M. rectus abdominis and the M. obliquus internus (origin).

N. *supracoracoideus* (12, Fürbringer) (n.s.cor.) arises at the point where the scapula and coracoid join, passes mesially, closely applied to the dorsal surface of the latter, and penetrates the For. supracoracoideum to the ventral surface. Here it divides into three branches, one branch supplying the M. procoraco-humeralis (p-h.) (14, Für.), another the MM. supracoracoideus and coraco-radialis proprius (s.c.) (13, Für.), while the third is a cutaneous branch to the skin over the neck and breast (cut.) (15, Für.).

It is this nerve which receives most of the anastomosis from the second spinal nerve.

At about this level, or a little later, N. spinalis 3 divides rather unequally into a larger anterior branch and a smaller posterior branch. The latter joins the main branch of the fourth spinal nerve to form the flexor nerve of the fore-limb (N. brachialis longus inferior, Fürbringer). The former, after receiving one or two small contributions from N. spinalis 4, passes to the dorsal side of the limb to innervate the extensor muscles (NN. brachiales longi superiores, Fürbringer).

N. *subscapularis* (n.s.sc.) (29, Für.) to the muscle of the same name leaves the anterior branch of the IIIrd nerve just before it receives its contribution from the IVth. It is a very fine nerve.

N. *dorsalis scapulae* (n.d.sc.) (30, Für.) frequently arises as two nerves—or as one nerve which divides almost immediately—and

passes round the posterior border of the scapula to its lateral surface, mesial to the M. dorsalis scapulae. The smaller posterior nerve goes entirely to the muscle. The larger anterior nerve gives a few small twigs to the muscle and then passes to its anterior edge, where it divides into three cutaneous and two muscular branches. The two latter enter the adjoining edges of the MM. dorsalis scapulae and procoraco-humeralis respectively, while of the cutaneous branches (*NN. cutanei brachii superiores laterales*, 32, Für.), one (α , Fig. 55) supplies the skin covering the lateral surface of the arm, while another (β , Fig. 55) turns mesially over the procoracoid to the skin of the breast, and the third (γ , Fig. 55) turns dorsally to the skin of the scapular region.

N. axillaris (n.ax.) (Osawa) is a fairly large cutaneous nerve arising close to the N. dorsalis scapulae. It passes out between the M. dors. scap. and the M. dors. humeralis, and supplies the skin covering them.

N. dorsalis humeralis (n.d.h.) (= N. latissimus dorsi, 34, Für.) arises from an anastomosis between N. spinales 3 and 4, and appears to receive fibres from both spinal nerves. It passes dorsalwards alongside NN. dors. scap. and axillaris and enters the M. dorsalis humeralis mesially.

The nerves arising from the brachial plexus distal to this point will be dealt with under the headings 'Extensor nerves' and 'Flexor nerves'.

Fourth spinal nerve (ventral branch) (n.sp.4).

The proximal part of N. spinalis 4, after emerging from the sub-vertebral muscles, gives one or two fine dorsal branches to the M. thoraci-scapularis (= N. thoracicus superior 4, Für.). Between this point and the plexus one or two fine branches are given off to the M. rectus abdominis.

Extensor nerves.

NN. brachiales longi superiores Fürbringer.

These consist of two¹ main nerves which enter the arm posterior to the humerus and shoulder-joint, passing between the heads of the MM. anconeus scapularis medialis and anconeus coracoideus in company with the Vena brachialis medialis. They pass to the dorsal side of the humerus.

¹ Fürbringer reports one anomalous case in which the extensor nerve in the arm was represented by a single large bundle, instead of the two parallel nerves found normally.

N. extensorius cranialis (n.ex.cr.). Sieglbaur (1904).

Musculo-spiral, or radial nerve	Humphry (1871).
N. radialis profundus	Fürbringer (1873); Hoffmann (1873-8); Ribbing (1907).
N. radialis superior	Osawa (1902).

This is the larger of the two extensor nerves and is the main continuation of *N. spinalis* 3. Immediately on entering the arm the nerve turns slightly anteriorly and gives a branch to the *M. anconeus humeralis lateralis*. It then passes obliquely across the limb between the *MM. anconeus humeralis lateralis* and *medialis*, remaining lateral to the humerus, and emerges at the surface of the muscle on the flexor side of the elbow. Here it gives a fairly large branch which spreads over the skin on the extensor surface of the fore-arm—the *N. cutaneus antibrachii dorsalis* (n.cut.abr.d.). A little farther on another cutaneous branch arises and passes right along the radial side of the fore-arm as far as the wrist, where it becomes known as the *N. dorsalis manus radialis* (n.d.m.r.). On reaching the carpus it divides, one small twig continuing along the radial side of the first digit, while the rest of the nerve crosses the wrist to the interdigital space between the first and second fingers. Here it divides again and supplies the skin on the adjoining sides of these two digits. Although mainly cutaneous, this nerve also sends a twig—soon after its origin at the elbow—to the *M. extensor antibrachii et carpi radialis*, and, as it crosses the carpus, it gives very fine twigs to the *MM. extensores breves digiti I and II*.

The main extensor cranialis nerve, after giving off these cutaneous branches, turns mesially and describes a half-spiral turn round the head of the radius, passing between this bone and the *M. extensor antibr. et carpi rad.*, so as to lie in the interosseal space between the radius and the ulna. As it passes over the radius it gives two twigs to the *M. extensor antibr. et carpi rad.*

About midway between the wrist and the elbow the nerve divides into two branches.

(a) The *N. dorsalis manus intermedius* (n.d.m.i.) which remains in the interosseal space, and passes along the fore-arm to the carpus, where it becomes more superficial, and lies directly under the *M. extensor digitorum communis*. From here it passes to the space between the second and third digits and bifurcates to supply the neighbouring sides of these two fingers. As it passes over the carpus the nerve supplies fine twigs to the *MM. extensores breves digitorum II and III*, and at the proximal part of the wrist, a larger

branch which supplies the MM. ext. brev. dig. I, and abductor digiti I.

(b) The second branch is the *N. dorsalis manus ulnaris* (n.d.m.u.). Almost immediately after its separation it receives one of the terminal branches of the *N. extensorius caudalis* (q.v.). It then runs along the fore-arm over the ulna, parallel with the previous branch, and gives off one or two twigs which pass outwards, between the MM. extensores antibr. et carpi radialis and ulnaris, to supply the M. extensor digitorum communis. From these twigs fibres may also pass into the M. extensor antibr. et carpi radialis. In the region of the wrist this nerve becomes more superficial and lies directly under the M. extensor digitorum communis, and, after giving off a branch to supply the skin on the ulnar side of the fourth digit, it crosses to the space between the third and fourth digits and divides to supply the skin on the adjoining sides of these two fingers. It also gives fine twigs to the MM. extensores breves digitorum III and IV.

N. extensorius caudalis (n.ex.cd.). Sieglbauer (1904).

Posterior ulnar, or better, inferior

musculo-spiral nerve

Humphry (1871).

N. radialis superficialis

Fürbringer (1873); Hoffmann (1873-8);

Ribbing (1907).

N. radialis inferior

Osawa (1902).

This is the smaller of the two extensor nerves and is separated from the anterior extensor nerve by the Vena brachialis medialis, but receives one or two fine anastomosing twigs from it. It arises more definitely from the *N. spinalis* 3-4 anastomosis than does the *N. extensorius cranialis*.

Soon after entering the arm it gives off a large cutaneous branch, *N. cutaneus brachii dorsalis* (n.cut.br.d.). This branch often carries some motor-fibres for the MM. anconaeus scapularis medialis and anconaeus coracoideus. Then follows a short branch which divides into three and supplies the scapularis medialis, humeralis and coracoideus portions of the anconaeus muscle, while a little farther on a small twig is given off to the M. anconaeus humeralis lateralis. Still farther distalwards another twig to the M. anconaeus coracoideus may frequently be found.

On reaching the flexor side of the elbow the nerve bends round the antero-lateral edge of the M. anc. hum. lat., and passes to the extensor side of the fore-arm, crossing obliquely over the origin of the M. extensor digit. comm., between the muscle and the skin. At the elbow it gives a cutaneous branch to the ulnar side of the fore-

arm, and then passes round under the *M. extensor antibr. et carpi ulnaris*—i.e. between this muscle and the ulna—into the interosseal space of the fore-arm. In doing so it supplies one or two twigs to the above-named muscle and finally gives a large anastomosis—amounting almost to the entire nerve in some cases—to the *N. dorsalis manus ulnaris*. The remainder of the nerve ends in the *MM. extensores antibr. et carpi radialis* and *ulnaris*.

The exact relation between the *NN. extensorius caudalis* and *cranialis* at this point is subject to some variation. In one case no certain anastomosis between these nerves in the fore-arm could be found. In this example both nerves were approximately equal in size all the way along, and the anterior nerve did not divide in the fore-arm but formed only the *N. dors. manus inter.*, while the posterior nerve ran parallel with it and formed the *N. dors. manus ulnaris*. If any fusion between these nerves occurred at all it was at the elbow-joint, in a similar position to that described by Sieglbauer (1904) for *Necturus*, but owing to the ribbon-like, translucent appearance of the nerves in this specimen, it was impossible to decide whether one was dealing with a nervous connexion or merely with the connective tissue capsule of the joint. In any case the anastomosis, if it did occur, was very fine and in no way comparable with the normal condition described above.

Flexor nerves.

N. brachialis (n.br.).

N. brachialis longus inferior Fürbringer (1873).

After receiving the anastomosis from the third nerve, *N. spinalis 4* gives off posteriorly *N. pectoralis* (n.pect.) to the pectoralis muscle. The *N. pectoralis* passes round the posterior border of the coracoid and enters the muscle on its mesial side. It is accompanied by a cutaneous nerve which supplies the skin covering the pectoral region. From about this level another cutaneous nerve arises, *N. cutaneus brachii superior medialis* (n.cut.br.s.m.) (42, Für.), supplying the skin of the axilla, and the postero-mesial aspect of the upper arm.

After giving off these branches, the brachial nerve (which forms the main continuation of the fourth spinal nerve) enters the arm ventral to the extensor nerves, posterior to the shoulder-joint, and between the *M. anconaeus coracoideus* and the *M. anconaeus scapularis lateralis*, and passes to the ventral side of the humerus. It then divides into a *R. superficialis* and a *R. profundus* (Fürbringer),

and at the same time describes a half-spiral turn so as to lie on the flexor side of the humerus, between the *M. coracobrachialis longus* and the *M. humero-antibrachialis inferior*. The two rami run parallel with one another separated by the *A. brachialis*. They are usually approximately equal in size, but the *R. super.* may be larger than the *R. prof.* Normally also this latter ramus passes to the elbow without branching, but one or two fine muscular twigs may be given from it.

At the point where these two nerves separate, or immediately afterwards, one or two branches are given off from the *R. superficialis* to the *MM. coraco-brachialis longus* and *brevis*; they are the *NN. coraco-brachiales* (*n.cor.br.*).

Then follow one or two cutaneous branches which pass out to the skin between the *M. coraco-brachialis longus* and the *M. humero-antibrachialis*. One branch longer than the rest travels along the arm to the elbow, and then takes a half-spiral turn to the lateral aspect of the fore-arm, crossing the origin of the *M. flexor primordialis communis* in doing so. These branches represent the *N. cutaneus brachii inferior lateralis* of Fürbringer, but are here called *N. cut. brachii inf. medialis*, to agree with the blood-vessels. The *R. superficialis* also supplies the *M. humero-antibrachialis inferior* with one or two fine branches.

At the elbow-joint it bifurcates. One branch remains superficial and passes along the skin on the radial side of the fore-arm and first digit. At the base of the finger it sends a branch mesialwards which supplies the short flexor muscles related thereto, and finally joins the *N. interosseus*. This branch of the *R. superficialis* would appear to represent Fürbringer's *N. cutaneus brachii inferior medialis*, here called *N. cut. brachii inf. lateralis*.

The other branch turns mesially, and passing under the *M. flexor antibr. et carpi radialis*, gives a small branch to this muscle, and finally joins the *R. profundus*. As already indicated this latter nerve passes right down the arm to this point without giving off any important branch. The nerves arising from this plexus will be termed *N. ulnaris* and *N. interosseus*.¹

N. ulnaris (*n.ul.*).

R. superficialis ulnaris McMurrich (1903).

This branch passes distally and obliquely across the fore-arm, deep to the *MM. flexor primordialis communis* and *flex. antibr. ulna-*

¹ Ribbing applies these names to the proximal portions (*R. superficialis* and *R. profundus*) also, but they seem hardly applicable to this region of the limb.

ris, but superficial to the *M. caput longum musculorum contrahentium*. When it arrives at the mesial edge of the latter muscle, at about the level of the middle of the fore-arm, it gives two muscular branches. The smaller of these divides into three to supply the *M. flex. prim. comm.* and the *MM. flex. antibr. et carpi ulnaris* and *radialis*. The other branch *R. medianus* (Ribbing) = *R. superficialis medialis*, McMurrich (*n.ul.r.m.*), passes along the mesial edge of the *M. cap. long. musc. contra.*, and appears to terminate at the point where the *M. flexor accessorius medialis* joins the tendon of the *M. flex. prim. comm.* It innervates the *M. cap. long. musc. contra.* and the *M. flex. acc. med.*

The main *N. ulnaris*, after giving off the *R. medianus* crosses the ulna, and, following the mesial border of the *M. flex carpi ulnaris*, emerges at the side of the arm between this muscle and the *M. flex. acc. lat.* At the proximal border of the *M. flex. acc. lat.* a twig enters the muscle, and as the nerve passes along its lateral border a fairly constant branch is given off to the skin. At the base of the fourth digit another cutaneous branch passes along the ulnar side of the finger, while the main nerve turns mesially again and crosses the base of the finger, between the *MM. contrahentes digitorum* and the *M. flex. brev. prof. IV* to the interdigital space of the third and fourth digits. Here it divides again into three main branches, of which two are distributed to the skin of the adjoining sides of the third and fourth fingers, while the remaining one crosses the base of the third digit, between the *M. contra. digit.* and the *M. flex. brev. prof. III*, to join the corresponding palmar branch of *N. interosseus*. Besides these cutaneous branches a number of small muscular twigs may be traced into the several short flexor muscles of the fourth digit, e.g. *M. contra. digit.*, *M. flex. brev. super. and prof.*, *M. flex. digit. min.*, and *M. interossei III-IV*.

N. interosseus (*n.io.*). Ribbing (1907).

<i>R. profundus</i>	McMurrich (1903).
<i>N. medianus</i>	Sieglbaur (1904).

This branch almost immediately dips down to the *dorsal* side of the *M. interosseus antibrachii*, and passes alongside the extensor nerves—*NN. dors. manus inter. and ulnaris*—in the interosseal space of the radius and ulna. It lies anterior—radial—to the *N. dors. manus inter.* There is no anastomosis between these nerves in the Salamander as there is in Triton (cf. Sieglbaur, 1904). During its course down the fore-arm it gives one or two twigs to the *M. interosseus antibrachii*, and also to the *M. pronator profundus*. The

nerve becomes more superficial again at the wrist, where it passes dorsal to the tendon of insertion of the *M. cap. long. musc. contra.*, between the basalia of digits 2 and 3. At the interspace of these digits it bifurcates and each ramus again divides into two, so that the posterior ramus supplies the skin on the pre-axial side of the third digit—*N. digitalis ventralis* 3—and also joins the terminal twig of the *N. ulnaris*, while the anterior ramus similarly innervates the post-axial side of the second finger—*N. dig. vent.* 2—and then passes across to the interspace of the first and second digits and supplies the skin of their adjoining sides—*NN. dig. vent.* 1 and 2—and finally joins the *N. cut. inf. lat.* It is not certain that this latter fusion is quite constant, but it certainly occurs in a sufficient number of cases to justify its being considered 'normal'. There is thus a complete nerve loop across the palm. The *N. interosseus* also innervates the short flexor muscles of digits 2 and 3 by small twigs in the appropriate places.

The ventral ramus of the *fifth spinal nerve* (*n.sp.5*), on emerging from the subvertebral muscles, divides into two branches, and the posterior one divides again several times to supply the various muscles of the ventral body-wall in that region. The anterior branch also divides again, one branch anastomosing with *N. spinalis* 4 and entering the brachial plexus, while the other is distributed to the skin of the axilla and the ventro-posterior side of the arm. This branch is usually joined by a branch arising direct from the plexus 3-4 which is somewhat variable in size, and in one case could not be found. The resulting nerve may be called *N. cutaneus brachii ventralis* (*n.cut.br.v.*).

Fürbringer seems to have overlooked this nerve unless it is represented by one of the 'Aeste für Bauchmuskeln' which he has not followed in detail. This author also figures a condition sometimes met with, in which the branch entering *N. spinalis* 4 bifurcates just before doing so, and sends a small twig to join the *N. pectoralis*. From this, and from the fact that the fifth nerve nearly always enters the fourth close to the point whence the *N. pectoralis* emerges, it seems safe to conclude that at least some fibres from the fifth spinal nerve normally contribute to the pectoral nerve.

6. Crural Plexus, and Nerves of the Hind-limb (Pl. XII).

The crural plexus of the Salamander is formed by the fifteenth, sixteenth, and seventeenth spinal nerves, with small contributions from the fourteenth and eighteenth. The main nerves of the plexus are

sixteen and seventeen.¹ It is noteworthy that, as compared with the fore-limb, the N. femoralis—from the fifteenth and sixteenth nerves—enters the limb *anterior* to its articulation with the pelvic girdle, while in the fore-limb no nerve passes into the arm in front of the glenoid cavity. With this exception there is a marked similarity between the two plexuses. For example, the N. obturatorius is strongly reminiscent of the N. supracoracoideus, or again, the extensor or dorsal nerves of the limb arise from the plexus anterior to the flexor or ventral nerves in both limbs. The comparison amounts almost to identity in the distal parts of the limb—a feature which is of course correlated with the close similarity of the musculature of the fore-arm and hand with that of the leg and foot.

The anastomosis with the fourteenth nerve is slight and involves only branches of the N. ileohypogastricus.

Fifteenth spinal nerve (ventral branch) (n.sp.15).

This nerve emerges from the penultimate trunk vertebra and passes obliquely postero-laterally towards the limb. Its first branch is an anterior one to the muscles of the lateral and ventral body-wall, the N. *ileohypogastricus* (n.il.hg.). The actual point at which this branch leaves the main nerve varies considerably in different specimens, since it may be either nearer to, or more distal from the vertebral column than shown in Plate XII, which is about the average position. At what may be termed the groin, i.e. in the anterior angle between the limb and the body, the remainder of the fifteenth spinal nerve divides into three. The first of these branches is the N. *cutaneus femoris medialis* (n.c.fm.m.) (Hoffmann) supplying the skin over the antero-dorsal region of the thigh. Hoffmann describes a branch to the M. ileo-extensorius from this nerve, but it has not been possible to confirm its presence, and it probably represents an individual variation. The remainder of the nerve has been called N. *cruralis anterior* by Hoffmann; it gives off the following two branches.

N. *obturatorius* (n.o.) passes ventrally through the M. pubo-ischio-femoralis-internus, supplying it with many twigs in doing so (p.i.f.i.), and finally penetrates the obturator foramen to innervate the anterior portion of the M. pubo-ischio-femoralis externus. The other branch fuses with the anterior branch of N. spinalis 16, to form:

N. *femoralis* (n.fm.). Osawa (1902); Sieglbaur (1904).

Anterior crural nerve	Humphry (1871).
N. cruralis	Hoffmann (1873-8).

¹ Sieglbaur gives the sixteenth, seventeenth, and eighteenth for the crural plexus, but he probably regards N. hypoglossus as N. spinalis 2.

This nerve passes into the leg penetrating the *M. pub. isch. fem. int.* to which it gives a few fine twigs. Just before entering the muscle it gives off a branch to the anterior portion of the *M. extensor iliotibialis* (e.i.l.t.). The nerve takes a rather winding course in the thigh, at first turning sharply posteriorly so as to lie close to the proximal end of the femur on its dorsal side. It then turns right round and proceeds along the limb, winding itself around the femur so that it lies directly anterior to it at the knee. At the antero-dorsal aspect of this joint the nerve becomes superficial to the muscles, emerging between the *M. pub. isch. fem. int.* and the *M. pubo-tibialis*, i.e. *dorsal* to the latter muscle. Several cutaneous branches arise in this region which Hoffmann takes to represent the *N. cutaneus femoris internus* (*saphenus minor*) (n.c.fm.i.).

The nerve then continues along the antero-dorsal border of the leg immediately under the skin as:

N. dorsalis pedis tibialis (n.d.p.t.). Sieglbaur (1904); Humphry (1871).

N. saphenus Osawa (1902); Ribbing (1908).

Just distal to the knee the nerve gives a small twig to the *M. extensor cruris tibialis* (e.t.t.), and, at about a third of the distance between the knee and the ankle, another branch penetrates the same muscle. A considerable proportion of this branch is cutaneous and passes right through the muscle to reappear near the middle line on the dorsum of the leg, but a number of fibres do actually terminate within the muscle itself.

Ribbing (1908) was the first to call attention to the motor-fibres in the *N. dors. ped. tib.* (his *N. saphenus*), and they are not common to all Urodeles.

Numerous cutaneous branches are given off to the skin on the mesial and dorsal sides of the leg and foot.

At the base of the first digit the nerve divides, one twig—*N. digitalis dorsalis 1* (n.d.d.1)—passing along the pre-axial side of the first toe, while the other crosses the base of the digit dorsally and then divides into two so as to supply the adjoining sides of the first two digits—*NN. digit. dors. 1* and *2*.

The relations of the *N. femoralis* vary considerably in different specimens, and particularly with regard to the point at which it emerges from the thigh muscles. This usually occurs at the knee as described, while it may emerge much nearer the body, but in any case its course through the thigh forms a half-spiral turn. The

close correspondence between the course of the N. dors. ped. tib. in the leg and that of the N. dors. man. rad. in the fore-arm is obvious.

Sixteenth spinal nerve (ventral branch) (n.sp.16).

This nerve emerges from the last trunk vertebra and passes somewhat obliquely postero-laterally across the dorsal pelvic region to the posterior border of the acetabulum, and there splits into two more or less equal parts. The anterior portion, which however may be much smaller than the other, turns anteriorly to join a branch from the fifteenth spinal nerve and form the N. femoralis as described above, while the posterior branch enters the limb close to the seventeenth nerve immediately behind the hip-joint. It anastomoses closely with N. spinalis 17, but nevertheless its main continuation in the thigh is the *N. extensorius* (n.e.) (cf. N. spin. 3, in brachial plexus). The *N. ischiadicus ventralis* (n.i.v.) also receives a considerable proportion of its fibres from the sixteenth spinal nerve.

N. extensorius (n.e.).

N. fibularis	Hoffmann (1873-8);	Appleton (1923-8).
N. peroneus	Sieglbaur (1904).	

After its formation from NN. spin. 16 and 17 the extensor nerve passes dorsal to the M. iliofemoralis, and gives a twig to it, and then divides into two rami which pass along the thigh parallel with one another immediately ventral to the MM. iliofibularis and extensor iliotibialis. They supply these muscles (il.f. and e.il.t.), and give off one or two cutaneous branches which probably represent the *N. cutaneus surae lateralis* (n.c.s.l.), while they also send a fine twig to the knee-capsule. The two rami reunite proximal to the knee to form a single nerve, or in some cases the nerve remains single throughout. At the knee-capsule it becomes:

N. peroneus (n.pn.).

This nerve leaves the thigh *dorsal* to the M. iliofib., and, executing a half-spiral turn, enters the leg, passing ventral to the M. femoro-fibularis between this muscle and the fibula. During its passage under the skin, superficial to the origin of the extensor cruris et tarsi fibularis, it gives off one or two muscular branches which enter this muscle (e.c.t.f.) on its post-axial side. The nerve passes to the interosseal space of the tibia and fibula, and there divides into two principal rami which correspond to the NN. dors. man. inter. and ulnaris in the fore-arm. They have accordingly been named by Sieglbaur *N. dorsalis pedis intermedius* (n.d.p.i.) and *N.*

dorsalis pedis fibularis (n.d.p.f.). The *N. dors. ped. fib.*—the post-axial branch—almost immediately divides again and gives off a branch which passes along the leg between it and the *N. dors. ped. inter.* It innervates the *M. extensor digitorum communis* (e.d.) and *MM. extensores breves digitorum* 3 and 4 (e.b.3 and e.b.4) and sends a large branch to join the *N. dors. ped. inter.* This ramus is not mentioned by Sieglbaur. It is named here *R. accessorius n. dorsalis pedis fibularis* (n.d.p.f').

A comparison with the fore-limb suggests that the essential difference between it and the hind-limb is that in the former case the anterior and posterior extensor nerves remain separate until distal to the elbow-joint, so that the extensor communis muscle and the ulnar extensor muscles are innervated by sundry twigs from both the *N. ext. caudalis*, and from the *N. dors. man. ulnaris*—a branch from the *N. ext. cranialis*. In the hind-limb, however, the anterior and posterior extensor nerves of the thigh unite proximal to the knee to form a single trunk which redivides in the leg, so that the extensor communis muscle and the fibular extensors are innervated by the *N. dors. ped. fib.* and its *R. accessorius*, which separate from the *N. dors. ped. inter.* as a single bundle. A comparison of Plates XI and XII will make this clear.

The *N. dorsalis pedis fibularis* (n.d.p.f.), after separating from the *R. accessorius*, passes down the leg along the extensor side of the fibula, immediately deep to the *M. extensor cruris et tarsi fibularis*. It innervates this muscle by several twigs (e.c.t.f.). At about the level of the distal end of the fibula it receives an anastomosis from the *R. accessorius*, while at the distal edge of the *M. extensor cruris et tarsi fibularis* it gives off a cutaneous branch to the skin of the post-axial side of the fifth digit—*N. digitalis dorsalis* 5. The remainder of the nerve crosses the base of this toe, giving a muscular twig to the *M. ext. brev. digit. 5*, and then divides to supply the adjoining sides of digits 4 and 5—*NN. digitales dorsales 4 and 5*.

N. dorsalis pedis intermedius (n.d.p.i.). This comparatively large nerve passes along the interosseal space of the tibia and fibula to the tarsus. It lies immediately posterior to the *N. interosseus*, and during this part of its course it innervates the tibial extensor muscles, viz. *M. extensor tarsi tibialis* (e.t.t.), and *M. extensor cruris tibialis*, the latter twigs coming off near the origin of the nerve. At the ankle it gives twigs to the *M. abductor et extensor digiti 1* (a.e.1), and to the *MM. ext. breves digitorum* of the second digit (e.b.2). The nerve then divides into two, one branch—the anterior—supplying the adjoining sides of digits 2 and 3—*NN. digitales dors.*

2 and 3—while the posterior branch is similarly distributed to digits 3 and 4, forming *NN. digitales dorsales 3 and 4*. The posterior nerve also receives an anastomosis from the R. accessorius n. dors. ped. fib.

N. ischiadicus ventralis (n.i.v.). Appleton (1928).

Arises from a 16–17 anastomosis as a nerve of moderate size. It passes *ventral* to the M. caudali-femoralis, between it and the M. pubo-ischio-femoralis externus. It first gives one or two small branches to the M. ischio-femoralis (is.fm.) and then turns antero-ventrally between the M. caud. fem. and M. pub. isch. fem. ext., giving off a large twig to supply the MM. pubo-ischio-tibialis (p.i.t.), pubo-ischio-femoralis externus (p.i.f.e.), and ischio-flexorius (pars propria) (is.f.). It then turns more anteriorly and gives off a large musculo-cutaneous branch. The cutaneous elements go to the skin covering the antero-ventral surface of the leg and form part of the *N. cutaneus femoris ventralis* (n.c.fm.v.). They emerge between the M. pub. isch. tib. and the M. pub. tib., while the muscular twigs supply the M. pubo-tibialis (p.t.). The nerve also gives at, or near, this point a small branch to the M. pubo-femoralis (p.fm.). The remaining portion of the N. isch. vent. now becomes the *N. cutaneus femoris ventralis* (n.c.fm.v.), and passes along the thigh to the knee between the muscles pubo-tibialis and pubo-ischio-tibialis. At the knee it becomes superficial and passes right along the tibial border of the fore-leg beneath the skin. It is continued to the extremity of the first digit as the *N. digitalis ventralis 1* (n.d.v.1). At the base of the digit it sends a branch mesialwards over the skin of the sole of the foot, from which a twig may arise to anastomose with a terminal branch of the N. interosseus, thus completing a plantar nerve loop corresponding with the palmar loop of the hand. It is very doubtful whether this anastomosis is a constant feature, since, when present, it is always exceedingly fine and difficult to dissect without breaking. The N. cut. fem. vent. may receive a branch from the sciatic nerve in the popliteal region, but this also does not seem to be constant.

Seventeenth spinal nerve (ventral branch) (n.sp.17).

N. spinalis 17 emerges from the sacral vertebra and passes almost transversely to the posterior border of the acetabulum, where it joins the sixteenth nerve, and, after anastomosing with it, continues into the leg as the sciatic nerve, from which arise the ventral or flexor nerves of the leg.

At the point where it joins the sixteenth nerve a branch arises from the posterior edge of *N. spinalis* 17 which supplies the muscles attaching the tail to the pelvic girdle. This branch is *N. pudendus* (n.pd.). A little distal to this nerve one or two cutaneous branches are given off to the skin covering the ventro-posterior region of the thigh—they are the *N. cutaneus femoris posterior* (n.c.fm.p.).

N. pudendus (n.pd.). Appleton (1928).

Leaves the seventeenth spinal nerve, as above described, just proximal to its junction with the sixteenth, and passes posteriorly mesio-dorsally to the *M. caudali-femoralis*. Almost immediately after its origin it gives one or two fine cutaneous branches to the postero-dorsal side of the leg. They pass dorsal to the *M. caud. fem.* and form part of the *N. cut. fem. post.* At about the same level a branch from the eighteenth spinal nerve enters the *N. pudendus*. The latter nerve then divides into four terminal branches, of which one enters the *M. caudali-femoralis* (cd.fm.), another supplies the *M. caudali-pubo-ischio-tibialis* (c.p.i.t.), and from this a cutaneous branch passes between the two muscles above-named to the skin at the side of the cloaca. Another branch passes to the cloacal gland in the male—or to the equivalent tissue in the female—between the *MM. caud. pub. isch. tib.* and *ischio-caudalis*, giving a small twig to supply the latter muscle in passing (is.cd.). This nerve would appear to be the *N. perinealis* (n.pe.) of Appleton. It is larger and better seen in the male.

N. sciaticus (n.s.).

Sciatic nerve	Humphry (1871).
<i>N. ischiadicus</i>	Hoffmann (1873-8).
<i>N. tibialis communis</i>	Osawa (1902).
<i>N. tibialis</i>	Appleton (1928).

The sciatic nerve passes down the thigh in company with the sciatic artery, and, a little proximal to the knee, gives off the following branches. First, one or more cutaneous branches which leave the thigh between the *MM. pub. isch. tib.* and *isch. flex.* and supply the skin covering the ventral (flexor) surface of the leg distal to the knee; they represent the *N. cutaneus surae medialis* (n.c.s.m.). One of these nerves—when there is more than one present—passes either close to, or through the 'pars plantaris' of the *M. ischio-flexorius* and supplies it with a small twig (is.f'). The other branch, which leaves the sciatic nerve near these cutaneous branches, is a muscular one. It divides to supply the *M. femoro-fibularis* (fm.f.),

and then enters the *M. flexor primordialis communis*. It may terminate within this muscle or it may pass right through and fuse with the *N. fibularis* (as figured, Pl. XII). In the latter case a branch passes from it to supply the muscle (f.p.). As already mentioned an anastomosing branch may pass from the mesial side of the sciatic nerve in this region to join the *N. cut. fem. vent.*

At some point between the hip and the knee the sciatic nerve splits to allow the sciatic artery to pass through it, but the actual extent of this split is subject to great variation. It may be quite short, when it occurs just proximal to the knee, or it may be of moderate length, as in the figure (Pl. XII). On the other hand, one case has been observed in which two approximately equal nerves, representing the sciatic, passed down the thigh parallel with one another, and with the sciatic artery between them. One of these nerves was derived from *N. spin. 17* and the other from *N. spin. 16*. They fused at the knee. This case, therefore, offers an explanation of the phenomenon of an artery penetrating an apparently solid nerve, and at the same time explains the variation in length of the split in different specimens, since this is merely a measure of the degree of fusion between the sixteenth and seventeenth nerves.

The whole sciatic nerve leaves the thigh *dorsal* to the *M. flex. fib.*, and enters the leg between the insertion of the *M. pub. isch. tib.* and the origin of the *M. flex. prim. comm.* Here it divides—if it has not already done so just proximal to the knee—and the divisions correspond very closely to the branches of the *N. brachialis* in the fore-arm. They have, therefore, been given analogous names in spite of the fact that the term '*N. fibularis*' has been applied by some authors to an entirely different nerve—viz. *N. peroneus*. Thus the two main divisions of the sciatic nerve distal to the knee are here called *N. fibularis* and *N. interosseus*, while the mesial branch of the *N. fibularis* is termed *R. medianus* since it corresponds with the similarly named branch of *N. ulnaris* in the fore-arm.

N. fibularis (n.f.) (*mihî*).

External popliteal	Humphry (1871).
R. lateralis n. ischiadici	Hoffmann (1873-8).

This nerve is not to be confused with Hoffmann's '*fibularis*', which is the dorsal or extensor nerve and the equivalent of the nerve here described under the name '*peroneus*'. As stated above, the close similarity between the nerve now under consideration and the *N. ulnaris* in the fore-arm seems to the writer sufficient justification for giving it an analogous name.

It passes down the fibular side of the leg deep to the M. flexor primordialis communis, between this muscle and the M. flexor accessorius medialis. Directly after separating from the N. interosseus the fibular nerve gives off a *R. medianus* (n.f.m.), which passes along the mesial—pre-axial—side of the M. cap. long. musc. contra. It innervates this muscle (c.l.c.), as well as M. flex. acc. lat. (f.a.l.), and terminates finally in the M. flex. acc. med. (f.a.m.). Just after it separates from the N. fibularis it gives a small twig to the M. plant. super. minor (pl.") of Eisler.

The main N. fibularis lies post-axial to the M. cap. long. musc. contra., close to the fibula. It may send a twig to the M. cap. long. musc. contra. (c.l.c.), but its main function is to innervate the M. flex. prim. comm. (f.p.c.), and the short flexor muscles of the fifth digit (a.d.5 and e.b.5). It also gives a cutaneous branch to the post-axial side of the fifth toe, N. digit. vent. 5. An anastomosis between a terminal branch of this nerve and one from the posterior ramus of the N. interosseus is usually demonstrable.

N. interosseus (n.io.) (*mihi*).

Internal popliteal	Humphry (1871).
R. medialis n. ischiadici	Hoffmann (1873-8).
N. tibialis medianus	Sieglbaur (1904).

This branch passes down the leg in the interosseal space between the tibia and fibula *dorsal* to the M. interosseus cruris. It supplies this muscle (i.c.), as well as the M. pronator profundus (p.p.). It appears again from beneath the muscle at the tarsus, between the tarsal bones of the second and third digits, but remains dorsal to the tendinous insertion of the M. cap. long. musc. contra. In this region it divides into three. One branch passes directly to the interdigital space of the second and third toes, where it bifurcates into the NN. digit. vent. 2 and 3, and the other two branches (which would seem to correspond to Humphry's anterior and posterior tibial nerves) similarly form the NN. digit. vent. 1 and 2, 3 and 4, and also 4 and 5, and in addition give twigs to all the short flexor muscles of these digits. The post-axial branch usually joins a terminal branch from the fibular nerve, while the pre-axial twig may—but probably does not always—anastomose with one from the N. cut. fem. ventr.

It should be noted that, in the Salamander, there is no exchange of fibres between this nerve and the dorsal, or extensor, nerves as there is in many Urodeles.

The *ventral ramus* of *N. spinalis* 18 bifurcates, immediately after penetrating the ilio-caudalis muscle, and the anterior portion passes

forwards inside the tough fibrous sheath surrounding the rectum, and anastomoses with the N. pudendus from the seventeenth spinal nerve.

The posterior ramus turns caudad, and sends a twig to the M. ilio-caudalis (il.cd.), and then penetrates the sheath to supply the cloacal gland in the male, or the homologous tissue in the female.

The *ventral ramus of N. spinalis 19* besides supplying the sub-vertebral muscle also supplies the cloacal gland.

The remaining spinal nerves, or *caudal nerves* as they may be termed, show gradual reduction in size and complexity towards the end of the tail, but are not characterized by any other special modification.

SYMPATHETIC NERVOUS SYSTEM¹

1. Historical.

Only three papers have been published on the sympathetic nervous system of *Salamandra*. The first, and best known, is by Andersson (1892). It is somewhat incomplete, but he gives an elaborate figure which illustrates the general relations of the abdominal and caudal portions very well, though the direct connexion he shows with the vagus ganglion must be considered doubtful, while his statement that a cranial sympathetic is entirely wanting is without doubt erroneous. The next account, by Jaquet (1900), is obviously based on Andersson's and suffers from the same defects. In 1902 Hoffmann's paper appeared on the development of the sympathetic system in *Salamandra*. This work adds several important details to Andersson's account, the most notable of which are the intimate association between the sympathetic nerves and the adrenal bodies (Nebenniere) and the close connexion of the latter with the veins. He denies that the sympathetic chain has any *direct* connexion with the vagus ganglion, and says that it terminates anteriorly with the ramus communicans to the first spinal nerve. From this point it travels mesialwards along the ventral ramus of this nerve, separates from it again at the point where it leaves the dorsal ramus, and passes forward to the vagus ganglion through the spino-occipital muscles. This certainly misrepresents the facts as far as the adult is concerned, since the anterior continuation of the sympathetic beyond the ramus communicans to the first spinal nerve is easily demonstrable by dissection under the binocular microscope, while

¹ It must be noted here that the term 'sympathetic' is used in the *anatomical* sense, and is not intended to include the system as a whole, which is more correctly called the *autonomic nervous system*.

the connexion described by Hoffmann between the vagus ganglion and the first spinal nerve is doubtless identical with that interpreted here as the spino-occipital nerves (see p. 156).

2. Description.

Following Andersson's arrangement, it is most convenient to describe the system in three sections, viz. (i) the *cephalic portion*, anterior to the ramus communicans to N. spin. 1, (ii) the *cervical and abdominal portions* continuing from the posterior extremity of the cephalic portion to the commencement of (iii), the *caudal portion*, lying within the haemal canal. It is further convenient to describe sections (ii) and (iii) before dealing with the more difficult and obscure cephalic section.

(ii) The *cervical and abdominal portions* (Pl. XVII, fig. 64). In general arrangement the sympathetic system consists of ganglia arranged in a paired longitudinal series on either side of the dorsal aorta, connected serially with each other by a chain of nerve fibres, and transversely with the ventral rami of the spinal nerves by the *rami communicantes*. There are also several cross-connexions between the two longitudinal series which will be mentioned subsequently.

The most anterior ganglion of this section—i.e. the one receiving the r. comm. n. sp. 1—is very small, as also is the next, but the third ganglion, lying immediately anterior to the subclavian artery, is a large one. It receives the r. comm. n. sp. 3. This section is called by Andersson the *cervical portion*. Anastomoses between the two sides occur in this region, both dorsally and ventrally to the aorta, and they usually pass obliquely from the second to the third ganglia. The nerve chain of each side in this section is usually double, and often treble, while sometimes it becomes so subdivided that it almost disappears.

The ganglion associated with the r. comm. n. sp. 3 is the *anterior subclavian ganglion* (Andersson) and from it emerge three, or sometimes four, nerves. Two of these pass to the *gang. subclav. postr.* (Andersson), one lying dorsal, and the other ventral to the subclavian artery. The dorsal nerve is very much stouter than the ventral. The third constant branch is a lateral one passing along the anterior side of the subclavian artery to the fore-limb. On the animal's right side this nerve bears a small ganglion situated about a millimetre from the dorsal aorta. This ganglion has not been observed on the left-hand side. It is usually connected with the posterior subclavian ganglion by a fine nerve which crosses the sub-

clavian artery obliquely. The fourth, and more variable, branch to leave the gang. subclav. antr. is an *anterior visceral nerve*, which passes alongside the anterior gastric artery to the stomach. This also seems to occur more frequently on the right side than on the left. Where the anterior visceral nerve does not separate from the anterior subclavian ganglion, it does so from the posterior one. The nerve described by Andersson as leaving the nerve strand just in front of the gang. subclav. antr. and entering N. tr. intest. X has not been found.

It may be noted here that the *rami communicantes* from the first six spinal nerves are not easy to see, since they frequently leave the nerve while it is still within the subvertebral muscles, and pass mesially through them to emerge close to the vertebral column. Andersson fails to find any r. communicans from the fourth spinal nerve, but it is certain that such exists in the majority, if not in all cases.

The *ganglion subclavius posterior* (g.scl.p.) marks the anterior end of the abdominal portion of the sympathetic chain. It is fairly large and frequently gives rise to the anterior visceral nerves (n.vis.a.)—see above. The next two ganglia—five and six—are also large, and, like all the subsequent ganglia of this section, have adrenal tissue intimately associated with them. In this section also the ganglia and the adrenal tissue are very closely applied to the post-cardinal veins, and frequently envelop them like a sleeve. The longitudinal nerve-fibres run parallel with the veins, and there is also a tendency in this region, particularly in the anterior two-thirds, for the fibres to pass from one ganglion to another in a divided condition, so that the strand then appears to be double, treble, or in some higher multiple. Sometimes one of the smaller bundles may miss a ganglion and join the succeeding one, so that it is not possible to give an exact and detailed description of the chain which will serve for any specimen. Similarly with the ganglia, they also are very variable both in size and arrangement. They normally, but not invariably, occur at the points where the *rami communicantes* join the longitudinal strand. Bearing in mind the disjunctive condition of this region of the sympathetic chain in Selachians (Young, 1933), it is evident that *Salamandra* forms a truly intermediate type between this and the more regular and definite arrangement found in the Frog. There is a distinct tendency for the *rami communicantes* in the posterior region of the abdomen, i.e. in the region of the kidneys, to bifurcate and join the longitudinal chain at two points. This bifurcation may occur right at the point of separation from the spinal nerve, so that the *ramus communicans* then appears double. Whether this subdivision

represents the morphological separation of the pre- and post-ganglionic fibres has not been determined.

There are two regions of special interest in this section. The first is around the ninth and tenth ganglia from which the *middle visceral nerves* arise. These run in company with the arteries and are distributed to the gonads, spleen, intestine, &c. The details of the visceral ganglia have not been worked out, but it would seem permissible to refer to the tenth ganglion as the *coeliac ganglion*. Both sides communicate with one another in this region. The second region of special interest is what Andersson calls the *plexus iliacus*, but it seems preferable to use the term *renal plexus*, since this avoids any confusion with the spinal nerves. At the point where the post-cardinal veins leave the post caval the sympathetic crosses their *dorsal aspect* and comes to lie between the kidney and the post-caval vein, always remaining *ventral* to the aorta. In the male the association of the adrenal bodies and the sympathetic with the post caval and its tributaries seems to be closer than in the female, a fact which may possibly be correlated with the greater development of the vasa efferentia in the former sex. Proceeding posteriorly from this point the longitudinal strand becomes thicker and the ganglia rather larger, particularly in the male. At about the twelfth or thirteenth ganglion the strand divides very definitely into two, and, while they may be connected by fine strands, they do not re-unite to form a single strand until the posterior end of the kidney is reached. The more dorsal of these strands (sym.d.) remains associated with the dorsalaorta. It receives the rami communicantes and is ganglionated. It is always connected with the ventral strand by a pair of strong commissures, one lying anterior and the other posterior to the iliac artery. Connexions may also exist in other regions, but they are variable. The ventral strand (sym.v.) remains ventral to the aorta but dorsal to the post-caval vein, and thus continues the direct line of the anterior portion of the strand. It is also ganglionated and remains in close connexion with the adrenal bodies. At the posterior end of the kidney, around the bases of the superficial renal arteries, the two sides of these ventral strands anastomose freely, and form a plexus. The pair of extra large ganglia situated in this region virtually terminate the ventral strands, since a fine nerve leaves each ganglion and passes dorsalwards around the posterior margin of each kidney and joins the dorsal strand, which then enters the haemal canal and continues as the caudal portion. The pair of ganglia just mentioned apparently represent the large median cloacal ganglion described by Heidenhain (1890) for Triton, and although they remain paired and

are much smaller in *Salamandra*, it is interesting to note that nerve-cells do occur along the commissure joining the two sides, so that it is easy to see how the unpaired condition has arisen. Heidenhain describes the ganglion in the male only, but no appreciable difference between the sexes has been noticed in *Salamandra*.

The sympathetic nerve for the hind-limb leaves the ventral strand at the plexus around the iliac artery. Fine fibres leave both the anterior iliac ganglia and entwine the artery, finally uniting to form a single strand at the edge of the kidney. From about the point at which the longitudinal nerve strand divides into dorsal and ventral portions as described above, i.e. at about the twelfth or thirteenth ganglion, a fine nerve is given off which passes laterally, and apparently supplies Müller's duct and the Wolffian duct. It is larger in the female. There appears to be a nerve plexus around these ducts but the details have not been elucidated.

(iii) The *caudal portion* is relatively simple and consists of a double nerve chain lying along the caudal artery. The ganglia are approximately segmental in arrangement. Anastomoses between the two sides are fairly frequent—otherwise there are no special features to note.

(i) The *cephalic portion*. After receiving the ramus communicans from the first spinal nerve, at about the point where the systemic arches join to form the dorsal aorta, the sympathetic chain follows each systemic arch around the pharynx, remaining rather towards the posterior side of the vessel. On reaching the point where the A. pharyngea ascendens is given off the nerve is deflected along it, and a portion enters the hyomandibular trunk of the facial nerve close to the point where the ramus communicans from NN. IX and X is received, and where the R. alveolaris is given off. At this point also a few nerve-cells occur (cf. p. 146). Another branch of the sympathetic crosses over the systemic arch and follows the A. petrosa lateralis into the antrum. It has not been determined precisely what happens to it, but presumably it enters the trigeminus ganglion, and, passing by way of the ophthalmicus profundus and the ramus communicans V ad III, reaches the ciliary ganglion on the oculomotor nerve. This point, however, has not been definitely established. The portion of the sympathetic passing round the systemic arch also appears to be connected with the pharyngeal rami of the branchial branches of the vagus nerve—in fact this has been described by Drüner. The presence of nerve-cells along certain rami of the cranial nerves, and in the ganglion copulare and the palatine ganglion, has already been noted (cf. pp. 141, 145, 150-2).

The appearance of the nerve during its course round the systemic arch is very variable. Sometimes the fibres are so diffuse as to render their dissection a virtual impossibility, but in cases where they are amalgamated into a single, or at least into a double strand, a dissection of as much of the system as has been described above is by no means impossible, though not easy. An idea of the difficulty may be gauged from the measurements given by Hoffmann, who estimated that the diameter of the strand is at most 0.05 mm. and is frequently barely 0.035 mm.

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17, 19, 21, 22, 37, 45, 46, 52, 64, 65, 66, 78, 94, 101, 102, 113, 114, 115, 134, 135, 143, 144, 145, 146, 166, 187, 192, 199, 200, 201, 202, 208, 226, 235, 236, 250, 251, 262, 291, 292, 303, 304, 305, 306, 307, 308, 323, 333, 351, 374, 378, 404, 440, 441, 489, 510, 516, 524, 525, 537, 543, 544, 545, 551, 578, 579, 615, 619, 628, 629, 630, 631, 632, 634, 656, 658, 686, 698, 705, 725, 726, 727, 728, 731, 732, 738, 739, 759, 765, 794, 806, 807, 808, 809, 810, 828.

VI

THE VASCULAR SYSTEM

BLOOD-VASCULAR SYSTEM

I. THE HEART

1. Historical.

ONE of the earliest investigators to attempt to describe the structure of the heart of *Salamandra* is Fritsch (1869), but his work and figures are unsatisfactory. He omits the sinus venosus entirely, and figures the divisions of the truncus arteriosus wrongly. In 1873 Langerhans published a brief account of the inter-auricular septum which he wrongly described as perforate. Nine years later (1882), Boas published his classic work *Über den Conus Arteriosus und die Arterienbogen der Amphibien*, which included a general account of the heart as a whole, in both larva and adult. His work is well known and forms the basis of most text-book descriptions. Röse (1890) gives a general comparative account of the heart in vertebrates, including *Salamandra*, but has few original observations to make. He agrees with Langerhans that the auricular septum is perforate. Langer (1894) made a thorough study of the structure and development of the bulbus cordis and truncus arteriosus, and draws a comparison between these structures and those of fishes, particularly the Dipnoi. Greil (1903) has also studied the development of the truncus arteriosus, of which he gives a good account. The rather considerable gaps which thus existed in the available literature on the anatomy of the heart of *Salamandra* have been filled recently, to a large extent, by Züllich (1930). His account is detailed and illustrated by a number of very good figures. Unfortunately he does not seem to have investigated the venous trunks for himself, but has copied Wiedersheim's erroneous figures. Nevertheless he gives a good account of the systolic rhythm and discusses the separation of the blood.

As regards the physiological and functional aspects, the classic work of Brücke (1852) may be mentioned. He saw the ductus Botalli between the pulmonary and systemic arches, and realized that it was perforate. He further undertook injection experiments to try to find whether the venous blood was separated from the arterial, and came to the conclusion that very little, if any, such separation

occurred. He thought that the acute angle at which the ductus Botalli meets the systemic arch would cause the former to be closed when the pressure in the latter rose beyond a certain minimum, and thus an admixture of blood in the two arches would be prevented. Suchard (1902) continued and extended Brücke's investigations. He thought that separation did actually occur but that it was only partial. He experimented by injecting a coloured fluid into the ventricle of an anaesthetized animal and found that it first entered the pulmonary arch, and therefore concluded that the first blood to leave the ventricle at the commencement of the systole would likewise enter the pulmonary arch. More recently, Nakano (1913) and Haberlandt (1916) have conducted physiological experiments on the heart of the Salamander, but their results lie rather outside the scope of the present work. The experiments were mainly of an electrical nature and were designed to elucidate the nature and sources of the nerve stimuli controlling the heart movements. Züllich's contribution to the physiological aspect has already been mentioned and will be referred to again on p. 191.

2. Description (Pl. XIII, figs. 59 and 60).

The present investigation was commenced before Züllich's paper appeared, and it was decided to reconstruct the anterior end of the ventricle, bulbus cordis, and truncus arteriosus by the wax-plate method in order to elucidate the details of their structure. The following description is based on a study of this model and of the sections from which it was built, as well as on the dissection of other specimens.

EXTERNAL FEATURES.

The heart of the Salamander is relatively much smaller than that of the Frog, while the *ventricle* (ven.) is shorter and has a more rounded apex, which is displaced a little to the right of the middle line. As seen in the ordinary course of dissection in a fresh or preserved specimen, the anterior face of the ventricle, instead of lying in a transverse plane as in *Rana*, is inclined obliquely to the left, and the auriculo-ventricular opening, instead of being at about the same transverse level as the opening of the bulbus cordis, is posterior to it, while at the same time both auricles are displaced to the left. The *bulbus cordis*¹ (b.c.) arises from the right antero-ventral angle of the ventricle and is inclined slightly to the left. It expands distally, where it merges into a short, thick *truncus arteriosus* (t.a.), from which

¹ Often incorrectly described as the truncus arteriosus, see p. 189.

arise normally four arterial arches, although occasionally only three may be present. These arteries do *not*, as in the Frog, leave the truncus as a single vessel, divided internally, but are separate from the beginning, and although a certain amount of connective tissue envelops their bases, it is clearly distinguishable from the arterial walls. In this connexion Züllich is a little misleading, since he refers to a 'Truncus arteriosus dexter' and 'sinister' (cf. his Abb. 1 with Fig. 60 of this work).

The *auricles* (or *atria*), as already stated, are displaced to the left. They are separated from the ventricle by a deep groove—the *sulcus coronarius*—which is especially apparent from the ventral side. Dorsally it is covered by the sinus venosus. It is not usually possible to distinguish accurately, from the outside, the partition between the auricles—the *septum atriorum*—but the left auricle is considerably smaller than the right. The *sinus venosus* (s.v.) is a large triangular sac which may normally be seen from the ventral side, lying dorsally and to the left of the heart (right as viewed), although obviously the exact size and shape will depend mainly on the amount of blood it happens to contain. It is much larger than in the Frog. The apex of the sinus venosus is directed posteriorly and receives the post-caval vein, while the two ducts of Cuvier enter the basal angles. On removing the heart, or by turning the apex of the ventricle forwards so that the dorsal side may be seen, there are exposed to view the right ductus Cuvieri lying across the anterior rim of the ventricle, and the pulmonary vein passing forwards along the right margin of the sinus venosus to enter the left auricle.

INTERNAL DETAILS.

In the detailed description of the internal structure and relations of the several parts of the heart, the order followed will correspond with the course of the blood through that organ, namely, from the sinus venosus to the truncus arteriosus.

Sinus venosus (s.v.). The cavity is undivided and the walls are very thin and devoid of striped (cardiac) muscle elements. It joins the right auricle at the anterior, right-hand, basal angle, quite close to the point of entry of the right duct of Cuvier, and the cavities of the sinus venosus and the right auricle are there confluent. The opening—the *ostium venosum sinus* (Züllich)—is situated near the septum atriorum, and is guarded by a large single flap valve which forms an antero-dorsal outgrowth from the septum atriorum, and prevents regurgitation of the blood from the auricle to the sinus venosus. It lies to the left of the ostium.

The *pulmonary vein* (v.pul.) lies close against the dorsal wall of the sinus, and anteriorly it actually lies *within* the wall. It enters the left auricle at its extreme right dorsal angle. The opening is *not* valved, so that regurgitation of the blood into the vein can only be prevented by the contraction of the surrounding muscles of the auricular wall.

The *auricles* (aur.) are separated from one another by a septum composed of a muscular network covered on either side by the cardiac endothelium. Thus the septum within the meshes of the network is exceedingly thin, and frequently appears to consist merely of the double layer of endothelial cells. It is probably due to this construction that the older authors thought it was perforate. The walls of the auricles are also formed of a muscular network, but it is much denser, so that, although the thickness varies greatly, they are never so extremely thin as the septum atriorum. The inner surfaces of the walls of the auricles are not smooth, neither are the cavities entirely simple, since the muscle bands form numerous ridges, and even isolated trabeculae, which are detached from the wall for a greater or shorter distance, thus forming a number of small pits and cavities within the wall. This is particularly the case in the left auricle and the upper part of the right. Owing to this peculiar formation of the auricular walls certain bulges appear on the external surfaces of the contracted auricles which have been named 'recesses' by Röse. Thus the *recessus sinister* lies at the ventro-posterior portion of the left auricle, the *recessus dexter* is the right ventro-posterior part of the right auricle, the *recessus intermedius* is the main cavity, and the *recessus dorsalis* the right antero-dorsal portion of the same auricle.

The *auriculo-ventricular opening* is a single oval aperture with the long axis in the horizontal plane, and the free edge of the septum atriorum stretching along the short axis in a dorso-ventral direction. Thus the blood from both auricles has to pass through a single opening into the ventricle. Regurgitation is prevented by a pair of flap valves, one dorsal and one ventral. Nevertheless, in the specimen modelled, there is a hint of a double nature of the opening, since at its left end there is a shorter pair of valves, partially separated from the main large pair by a fold. It is perhaps not safe to generalize from a single specimen, and it is not practicable to detect this feature except from sections. In any case the valves must be regarded as a single pair from a functional point of view. Nevertheless it is interesting to note that Osawa describes two pairs of valves in *Cryptobranchus*, where the heart is much larger and the valves easier to see, and they consist of one large and one small pair.

The *ventricle* (ven.), like that of the Frog, is a muscular sponge with a central cavity, but the sponge is much less dense than in that animal, and the central cavity is comparatively smaller. From the work of Benninghof (1920-1) there would appear to be some order in the seeming chaos of muscle bands composing the sponge of the ventricle, but the questions raised by this author are too special to be entered into here. The blood in many places comes very close to the external surface of the ventricle, and in a freshly killed specimen it is clearly visible within the meshes of the sponge, as the ventricular wall is semi-transparent. The 'central' cavity does not extend any distance caudad of the auriculo-ventricular opening, and is a more or less L-shaped canal leading from that opening to the *bulbus cordis*. For particulars of the *vena cordis* see p. 191.

Of the rather complicated structure interposed between the ventricle and the aortae, often loosely referred to as the 'truncus arteriosus', only the distal portion is actually the truncus arteriosus, homologous with the ventral aorta of the fish. The proximal portion is the *bulbus cordis*.

The *bulbus cordis* (b.c.) is a long, narrow, slightly twisted tube, cylindrical at the ventricular end and expanding in a horizontal plane to a broad oval distally. It is delimited from the ventricle by the presence of three pocket valves which prevent the reflux of the blood into the ventricle. When closed each forms a cup with the convexity towards the ventricle. They are *non-muscular* and thin-walled, with but few trabeculae stretching across their concavity from the *bulbus* wall. The dorsal valve is distinctly larger than the other two. The limit between the *bulbus cordis* and the truncus arteriosus at the distal end of the former is also marked by pocket valves, of which there are four—two dorsal and two ventral. They are also *non-muscular* but are V-shaped rather than cup-shaped, and are prolonged some distance in a caudal direction along the wall of the *bulbus*, forming ridges thereon. This is especially pronounced in the case of the right dorsal valve which is contiguous with the so-called *spiral-valve*—or better *septum bulbi*—a longitudinal septum partially dividing the cavity of the *bulbus* into right and left chambers. The *septum bulbi* is much more rudimentary than in the Frog and does not extend any distance anteriorly into the truncus, and it is very doubtful whether it has any influence on the separation of the venous from the arterial blood (cf. p. 191 *et seq.*). It passes across the dorsal wall of the *bulbus* from *left* posterior to *right* anterior. The distal valves frequently have small knobs of hyaline cartilage of varying size embedded in them. They are also much thicker than the

proximal row, while numerous trabeculae pass across their concave aspects from the wall of the truncus. The bulbus cordis is cardiac in origin, its muscular walls being of the same nature as, and continuous with, the ventricle.

The *truncus arteriosus* (t.a.) represents a greatly shortened ventral aorta enclosed in a sheath of cardiac muscle which grows forwards round it from the bulbus, the tissue pertinent to the truncus itself being *arterial tissue* containing *unstriated* muscle-fibres. The sheath of cardiac muscle envelops the whole of the truncus posterior to the aortic arches, and it is prolonged in the middle line so as to form a strap passing between the carotid arches from the dorsal to the ventral side. On the dorsal side, within the cavity thus formed between the strap and the truncus, is the central lymph heart (cf. p. 260). Züllich did not realize the true significance of the lymph heart and strap, but describes it as an 'elastische Polster', and says (p. 205), 'Die funktionelle Bedeutung scheint lediglich die zu sein, das dieses elastische Kissen den abgehenden Arterien Schutz gegen Knickung gewährt, bzw. eine nachgiebige, federnde Abstützung gegen den dorsal darüberliegenden Ösophagus bietet.' He does not appear to have been acquainted with Greil's work, although he states that the 'Polster' contains lymph.

As regards the cavity of the truncus arteriosus, two regions are discernible; a short undivided section next to the bulbus cordis—the *truncus impar*—and the main section which gives rise to the eight aortae by the ingrowth of septa from its walls. These septa have received different names from various authors. Greil's nomenclature is adopted here, and it is not thought necessary to give other synonyms as they are quite obvious. The septum between the carotid arches is the *septum caroticum*; that separating the carotid from the systemic arch on either side the *septum carotico-aorticum*; the *septum aortico-pulmonale* divides the systemic arch from the 'third' arch, and the latter is in turn separated from the pulmonary arch by the *septum accessorium*. The *septum pulmonale* separates the right pulmonary arch from the left. It should be noted that there is no great prolongation of the horizontal septum so as to divide the chamber into a *cavum pulmo-aorticum* and a *cavum aortico-caroticum* as there is in the Frog. In fact there is no well-marked difference in the length of any of the septa, and they may not be quite symmetrical on the two sides. The septum pulmonale is the longest and is closely followed by the septa aortico-pulmonale and caroticum, while the septa carotico-aortica and the septa accessoria are shorter and approximately equal to one another in length.

A *V. cordis* from the ventricle enters the right ductus Cuvieri on its ventral aspect at the *right* margin of the ventricle.

3. Functional.

The problem of whether there is any separation of the oxygenated and de-oxygenated blood in the Salamander is a vexed one. As already mentioned, Brücke—who was one of the earliest workers to attack the question—came to the conclusion, as the result of injection experiments, that in all probability no such separation did occur, while Suchard, who followed him, thought that there was some slight separation. Noble (1925), as the result of injecting Indian ink into the pulmonary veins of a number of Amphibia, both Urodeles and Anura—but not *Salamandra*—came to the conclusion that in those animals which possessed lungs, two auricles and a septum bulbi, the oxygenated and de-oxygenated blood remained distinct, and that the former never entered the pulmonary arch, whereas in those Amphibia which are devoid of lungs, and in which the septum bulbi and inter-auricular septum have also atrophied to a greater or lesser extent, no such separation could be demonstrated. He therefore ascribed to the *septum bulbi* the important function of bringing about this separation. All injection experiments are open, to a varying extent, to the objection that it is impossible to execute them without causing traumatic shock to the heart, which is very sensitive to such stimulus. It is, therefore, difficult to be sure that one is obtaining a normal systolic rhythm under these conditions. Noble's results are consistent, and would seem to be as free as possible from this objection. Nevertheless they are susceptible of another explanation than that which he puts forward.

Züllich (1930) gives a detailed and tolerably complete account of the course of the blood through the heart in *Salamandra*, and concludes that while the blood from the right and left auricles does to a large extent remain distinct as it passes through the heart, the *septum bulbi* is in no way responsible for this—a conclusion with which the present writer is in agreement. A careful examination of the structure of the bulbus cordis and truncus arteriosus makes it impossible to conceive that the septum bulbi can have any effect whatever on the separation of the two kinds of blood in the Salamander, although it probably has in *Rana* and other Anura where it extends farther into the truncus impar.¹

¹ Since this was written a paper has appeared by Vandervael (1933) setting forth conclusions different from those given here. His experiments consisted of observing the circulation of the blood through the heart and arterial trunks of the Frog by means of

The course of the blood through the heart is briefly as follows. The left auricle fills before the right. The systolic rhythm commences with the sinus venosus, which empties itself completely into the right auricle, and, as a result, the inter-auricular septum is pushed over into the left auricle, which accordingly commences to discharge its contents into the ventricle. The two auricles then contract almost simultaneously, the left leading ever so slightly, and thus the blood from the left auricle passes into the proximal or left-hand side of the ventricle, and that from the right into the central cavity and distal or right-hand side. The first blood to leave the ventricle is that from the right auricle, then a mixture from both right and left auricles, and finally that from the left auricle only. Now the resistance offered by the several vessels leaving the truncus is not identical in each case. The greatest resistance is offered by the carotid arch, by virtue of its labyrinth, and the least by the pulmonary arch. As therefore, the systole spreads on the ventricle, the first blood to leave would enter the latter vessel, and the last would go to the head via the internal carotid artery. The difference in pressure between the pulmonary and systemic arches must be very slight since they are connected by a perforate ductus Botalli, but the actual *capacity* of the pulmonary system is relatively small, and hence it speedily fills and allows the greater part of the blood to flow into the other two arches.

Noble's experimental results, which are simply that none of the ink injected into the pulmonary vein ever entered the pulmonary artery, are thus easily explained without involving the septum bulbi at all. There is another important feature to be noted which seems to have been overlooked by previous writers, namely, that as shown on p. 274 the bucco-pharynx is as intimately concerned with respiration in the Salamander as the lung, and this region, although supplied mainly by the pulmonary arch, returns most of its blood into the jugular veins and hence into the *right* auricle, so that although the blood of the left side of the heart is *purely* oxygenated blood, that of the right side must also contain a considerable amount of oxygen. Thus, by virtue of this and the systolic rhythm, the spongy ventricle and the resistance of the carotid labyrinth, the Salamander possesses

transillumination from the bulb of an ophthalmoscope lamp placed under the heart. He observed no perceptible difference in the colour of the blood in the three arches, and also found that Indian ink injected into the pulmonary vein was distributed simultaneously and equally to each of the three arterial arches. He therefore concluded that the septum bulbi was not responsible for any selective distribution of the two kinds of blood, and in fact went further, and claimed that the blood from the right and left auricles does not remain distinct in its subsequent passage through the remaining portions of the heart.

a mechanism whereby the brain is assured of a supply of pure oxygenated blood from the left auricle, and the body and respiratory systems are supplied with a mixed blood, of which that going to the former contains rather more oxygen than that to the latter system.

This hypothesis, by discounting the importance of the septum bulbi of *Salamandra* in effecting such separation of the blood, does not explain why the septum should be absent from those *Amphibia* which do not possess lungs, nor indeed why it should be present in those which do. On the other hand it must be remembered that the septum bulbi is but an exaggeration of the tendency to become prolonged into ridges exhibited by all the distal valves. It seems therefore not improbable that the inception of the septum bulbi may be referred to similar mechanical stresses to those which, in the other valves of the distal series, occasion the development of small rods of hyaline cartilage (cf. p. 189). Whether this is so or not, a careful observation of the contracting heart and *bulbus cordis* makes it certain that the presence of the septum enables the *bulbus* to empty itself *completely* of blood, and thus ensures that the last drops of pure oxygenated blood shall be forced into the vessels. In the case of an *apulmonate* species, where the blood in the ventricle is homogeneously constituted with regard to oxygen, this complete emptying of the *bulbus* would be of much less importance. In the *Anura*, e.g. *Rana*, the septum bulbi has developed more extensively, and the septum principale of the *truncus arteriosus* approaches close to its anterior end, so that the 'spiral valve' is able to execute the additional function of ensuring more effectively than pressure alone can do that the blood carrying least oxygen shall be delivered to the pulmonary artery.

4. The Pericardium.

The heart is surrounded by a coelomic space, the *pericardial cavity*, which is bounded externally by a tough, fibrous, transparent membrane—the *pericardium*. The cavity is completely separate from the pleuro-peritoneal coelom, there being no trace of any pericardio-peritoneal canal.

The pericardium is attached to the heart at the anterior end of the *truncus arteriosus*, at the ductus Cuvieri close to their formation by the fusion of the venous trunks, and also to the dorsal wall of the *sinus venosus* and to a part of the dorsal wall of the ventricle. This attachment of the ventricle to the pericardium is an annular one, involving a relatively large area (see Fig. 59). It is also present in the *Dipnoi* and in many *Reptiles*¹, but only as a ligamentous strand. In

¹ Cf. also Hoffmann in Bronn's *Thierreich*, Band VI, *Reptilia*.

these latter animals Fritsch (1869) calls the ligament the 'Gubernaculum cordis'. It is, of course, the remains of the dorsal mesocardium and is frequently referred to as the *mesocardial ligament*. The extensive area involved by this pericardio-ventricular connexion in Salamandra must be regarded as a very primitive feature. The auricles are free, as is also the whole ventral surface of the heart, except at the anterior end of the truncus arteriosus, at the ductus Cuvieri, and at the post-caval and pulmonary veins.

The pericardium has also important connexions with the MM. obliquus internus and rectus abdominis, which are discussed on p. 270 in relation to the question of the diaphragm.

II. BLOOD-VESSELS.

1. Historical.

Funk (1827) is neither accurate nor detailed regarding the blood-vessels—a situation that Rusconi (1854) made a special point of amending. Rusconi's figures of the aortic arches in both larva and adult are very good and are reproduced by Hoffmann in Bronn's *Thierreich*. He does not describe the remainder of the arteries in any detail, but he gives some account of the main veins, and is the first to describe the vessel derived from the left vitelline vein which now bears his name, but was called by him the longitudinal gut vein. Jourdain (1859) gives a good description, with figures, of the renal-portal system, but he figures the connexion between the V. iliaca communis and Jacobson's vein wrongly.

The first investigator to study the vascular system of the Salamander apart from the general anatomy was Hochstetter (1888). He gives a very good account of the veins of the abdomen and of the renal-portal system, but does not deal with the details of the cephalic vessels nor with those of the limbs. He recognized the true nature of the post-cardinal veins (Rusconi had called them the veins of the oviduct), and his work on the development of these vessels and of the abdominal vein is too well known to need comment. In 1894-5 Zuckerkandl, in his work on the anatomy and development of the arteries of the fore-arm, deals with Salamandra as a type of Urodeles, but his description is brief. Bethge (1898) supplements Hochstetter's account to some extent in a paper entitled 'Das Blutgefäßsystem von Salamandra maculata, Triton taeniatus, und Spelerpes fuscus'. He is the first to mention the vertebral artery—A. vertebralis collateralis—and the lateral vein—V. cutanea magna—but on the whole his description is very general. He is more concerned

with the respiratory function of the vessels he is describing than with their exact anatomical relations. He improves on existing accounts by giving some description of the vessels of the head region, but in this he is not quite accurate. He figures the lingual vein as passing *ventral* to the arterial arches and says that it breaks up into a 'Rete mirabile' in the region of these vessels.

The only vessel that can be identified with the vein he describes is the *V. thyroidea*, while the 'Rete mirabile' must be the thyroid gland itself. It is astonishing that he should have fallen into this error, as the development of the thyroid gland had been well described only four years previously by Maurer, but his figure allows no other explanation, since the thyroid vein is the *only* vein in that region passing *ventral* to the aortae. Bethge accurately figures and describes the proximal portion of the true lingual vein—which passes *dorsal* to the arterial arches—as the *V. pharyngea*.

Only two more authors need be noted here, namely, Choronshtsky (1900) who gives a good account of the development of the mesenteric veins and of the hepatic portal system, and Konigstein (1903) who describes the pulmonary and related arteries.

The vessels of the brain were first described by Schölb in 1882. His figures are very beautiful but not quite accurate, particularly in respect of the veins, and his work was amended later by Rex (1893).

2. General Features.

The condition of the blood-vascular system in the Salamander is extremely interesting, and it is surprising that no really adequate account of it exists, for we have in one and the same animal what amounts to two systems of blood-vessels—that of the fish and of the land vertebrate, and particularly is this so in the case of the venous system. The Salamander thus forms a nearly perfect transitional type, being in this respect much less specialized than the Frog.

The chief features of interest may be tabulated thus:

ARTERIAL SYSTEM.

- (i) Persistence normally of four arterial arches in the adult.
- (ii) Occurrence of a *perforate* ductus Botalli between the pulmonary and systemic arches.
- (iii) Limitation of the area served by the carotid arch.
- (iv) Distribution of a branch of the systemic arch to the palate.
- (v) Distribution of branches of the pulmonary arch to the oesophagus and pharynx.

VENOUS SYSTEM.

- (i) Persistence of the post-cardinal veins, which may even in some cases retain their primitive connexions with Jacobson's veins.
- (ii) The persistence of one of the *vitelline veins* of the embryo—the left—in a perfectly functional condition (see Rusconi's vein, p. 238).
- (iii) The obvious derivation of the venous system of the head from Selachian-like sinuses.
- (iv) The occasional absence of the middle portion of the post-caval vein, and corresponding enlargement of one of the post-cardinals.

As might be expected in an animal retaining so many primitive features there is a considerable amount of individual variation to be met with, and it is difficult to give a general account which will cover all cases, but it is hoped that the following description, based mainly on the dissection of specimens which have been injected with Prussian blue (gelatine and liquid) injection masses, will enable all the important vessels to be identified and followed.

All vessels may be taken as paired unless definitely stated to be otherwise.

The vessels of the cranial and vertebral cavities, both arteries and veins, are described at the end of the present main section under 'Vessels of the Brain'.

3. Arterial Arches (Pl. XIV).

The Salamander, after metamorphosis, normally retains all four of the branchial arteries present in the larva, and rarely three only are to be found. In the latter condition it is the 'third' arch which is missing, its place being occupied by a strand of pigmented connective tissue bearing the same relation to the M. cephalo-dorso-subpharyngeus and to the systemic arch as the artery does when present. The other arches present are—naming from anterior to posterior—(1) the *carotid*, (2) the *systemic*, and (4) the *pulmonary*.

The *carotid*—third visceral—arch (A. III) is not normally connected with the systemic by a ductus Botalli, but in one specimen such a connexion has been found on one side. It was exceedingly fine, however, and only just visible under the dissecting microscope.

The *systemic*—fourth visceral—arch (A. IV) is considerably larger in diameter than the other arterial arches while it also receives the blood leaving the heart by the 'third' arch. Its branches deliver blood

to nearly the whole of the body except the brain, the lungs, and the pharynx.

The *third*—fifth visceral—arch (A. V) varies considerably in size. Occasionally it is absent, or it may be quite well formed and comparable in diameter with the common carotid and pulmonary arches, but normally, however, it is much smaller. It leaves the truncus arteriosus somewhat postero-ventrally relative to the systemic arch, and, running parallel with the latter, ultimately fuses with it at the level of the dorsal side of the pharynx, just proximal to the entry of the ductus Botalli.

The *pulmonary*—sixth visceral—arch (A. VI) in the Salamander supplies the walls of the pharynx as well as the lungs. It does not run quite parallel with the other arches, but after leaving the truncus arteriosus it turns at first slightly posteriorly, then bends anteriorly to the anterior border of the M. dilatator laryngis, at which point the ductus Botalli is given off. The latter passes mesially to the muscle and enters the systemic arch just distal to the point where the 'third' arch enters. The ductus Botalli is perforated by a functional lumen, and in fact one or two small cutaneous branches are given off from it laterally, as well as the lateral pharyngeal artery from its mesial side. The pulmonary arch then turns sharply posteriorly again towards the lung.

4. Branches of the Carotid Arch (Common Carotid) (Pl. VI, figs. 37, 38, and Pl. XIV).

(NOTE.—The terms 'Internal' and 'External' are applied to the two divisions of the Common Carotid for sake of convenience, although their distribution is much more restricted than is the case in the Frog.)

The *common carotid* emerges from the truncus arteriosus somewhat antero-dorsal to the systemic arch and passes laterally for about 4 or 5 mm. to the carotid gland, where it divides into its external and internal branches.

A. The *external carotid* (a.car.e.) artery leaves the gland on its mesial side anterior to the entry of the common carotid, and runs back parallel with the latter for a millimetre or so before turning anteriorly. From this section of the vessel arises:

(i) *Ramus muscularis* for the MM. rectus cervicis and interhyoideus posterior. This branch divides almost immediately, so that the branch for the former muscle passes mesially, dorsal to the thyroid vein, while the other enters directly into its muscle, which covers this neighbourhood ventrally.

After turning anteriorly the carotid artery passes along the lateral border of the thyroid gland to which it sends:

(ii) The *thyroid artery*—a short but fairly broad vessel which breaks up immediately within the gland into a rich network.

On reaching the level of the second hypobranchial cartilage the main artery divides into three (sometimes four) branches as follows:

(iii) The *sublingual artery* (a.subl.), the more superficial of the two anterior branches, passes along the lateral border of the geniohyoid muscle to within about 3 mm. from the tip of the lower jaw. Here it divides into four rami.

(a) *R. lingualis* which passes mesially and enters the tongue together with the hypoglossal nerve.

(b) *R. muscularis* which passes anteriorly and enters the M. genio-glossus.

(c) *R. communicans* which passes laterally and sends a branch to the M. subhyoideus, then turning anteriorly and passing to the middle line round the lower jaw, where it may fuse with its fellow on the other side, although it may also anastomose with the mandibular artery. Whether these anastomoses always occur is uncertain, since failure to find them in every case may rather be due to faulty injections than to the absence of the vessels. They are very fine vessels.

(d) *R. intermandibularis* arises soon after the origin of the sublingual artery at the level of the first hypobranchial cartilage and passes ventrally into the underlying muscle of the same name.

(iv) The *lingual artery* (a.ling.), the other anterior branch, runs more or less parallel with the previous artery but *deep* to the geniohyoid muscle. It enters the tongue at two or three points between the radials of the copula, i.e. together with the glossopharyngeal nerve.

(v and vi). Two muscular branches which pass laterally to the lateral edge of the M. subarcualis rectus I, which they supply. These two branches may be represented at their origin by a single vessel for a greater or shorter distance.

All the branches of the external carotid artery are somewhat convoluted and very extensible—a necessary feature in view of the large amount of movement to which the parts they supply are subjected. They are only loosely held by connective tissue and are easily dissected. The external carotid artery as a whole has been called the *Arteria lingualis* by some authors—e.g. Hoffmann—but this would seem to be a misnomer.

B. The *internal carotid artery* (Pl. XIII, fig. 58; Pl. XIV, fig. 61) (a.car.i.) continues the direction of the common carotid as far as the floor of the otic capsule. Here it divides, giving off the *A. petrosa*

lateralis (a.pet.l.) (Drüner), which turns dorsalwards around the posterior border of the processus basilaris and enters the antrum petrosum laterale by the 'facialis' opening (see below). The remaining branch of the internal carotid then bends somewhat mesially across the ventral face of the Proc. basilaris and enters the *carotid canal* (Fig. 2, can.car.)—a groove in the floor of the cranium covered ventrally by the parasphenoid bone. There is no definite 'carotid foramen' in the Salamander's skull. The artery enters the cranial cavity through the *basicranial fenestra* and immediately gives off the *A. carotis cerebialis* (a.car.ce.) (Schölb.)—see 'Vessels of the Brain'.

The remainder of the vessel turns anteriorly along the edge of the basicranial fenestra as far as the foramen for the N. oculomotorius. It then penetrates this foramen and passes into the orbit as the *A. ophthalmica* (see next page).

(i) *A. petrosa lateralis* (Drüner) (a.pet.l.). This small but important vessel is probably to be regarded as the homologue of the stapedia artery of Mammals. As already described it passes into the *antrum petrosum laterale* around the posterior border of the processus basilaris, mesial to the corresponding vein, and ventral to the columella. Within the antrum the artery loops over the dorsal edge of the vein so as to lie lateral to it. It leaves the antrum between the Proc. oticus and the Proc. ascendens together with the mandibular and maxillary branches of the Vth nerve, and divides into the following two main branches:

(a) *A. temporalis* (a.t.), which accompanies the second division of the trigeminal nerve to the posterior angle of the eyelids, and here divides into two equal branches, one of which, the *superior orbital artery*, passes around the upper eyelid and anastomoses with the R. ophthalmicus superior posterior of the *A. ophthalmica*. The other turns ventrally and supplies the lower eyelid and the tissues of the posterior end of the upper jaw, and represents a portion of the *inferior orbital artery* (a.o.i.), the other part being represented by a branch of the *A. mandibularis*.

(b) *A. mandibularis* (a.m.). This branch of the *A. petrosa lateralis* turns ventralwards and accompanies the mandibularis branch of the trigeminus. Very soon after its origin it gives off a branch anteriorly, which passes through the levator mandibulae muscle and is distributed to the roof of the mouth at the postero-ventral corner of the orbit and also to the inflected portion of the skin which occurs in the coronoid region. This branch has not always been found, but failure to find it is more probably due to faulty injections than to its absence. It is very easily damaged in removing the muscle through which it

passes, and consequently may sometimes be overlooked. It can only be regarded as forming a portion of the inferior orbital artery.

In this connexion it is interesting to compare the relations found in the human embryo and in *Sphenodon* (see O'Donoghue, 1921, p. 192). In the human embryo the inferior orbital artery is given off from the mandibular branch of the stapedia artery, while in *Sphenodon* it is one of the two end branches of the A. temporalis. In *Salamandra* both these conditions are present in the one individual.

The mandibular artery proper continues ventro-laterally through the levator mandibulae muscle close to the nerve, and, like the nerve itself, divides on reaching the lower jaw into a *R. labialis* (Osawa) (a.lab.), to the skin on the lateral aspect of the posterior portion of the lower jaw, and a *R. alveolaris* (Osawa) (a.alv.), which passes through the inferior dental canal within the jaw itself to supply the teeth, &c.

In addition to the two main branches just described the A. petrosa lateralis gives one or two *RR. musculares* to the several portions of the M. levator mandibulae.

Abnormalities. Two rather interesting anomalies have been met with in this region, viz:

(1) A case in which the A. petrosa lateralis occurred as a branch of the A. pharyngea ascendens instead of the internal carotid, the latter vessel giving off no branch at all before entering the cranial cavity. The specimen was well injected, and the relations were quite distinct, while the branches of the A. petrosa lateralis were normal and both sides of the specimen were alike.

(2) A case in which a branch from the A. petrosa lateralis was given off almost immediately after its origin from the internal carotid to the lateral pharyngeal wall. This is the only trace that has been found of a pharyngeal artery stated by Bethge to occur as a normal branch of the internal carotid. Unfortunately the specimen was not injected, and the vessel was nearly empty of blood, so that its exact extent and relations could not be determined (see Fig. 58).

As already described the internal carotid artery terminates within the orbit as the *A. ophthalmica* (a.oph.). After leaving the cranial cavity by the oculomotor foramen the ophthalmic artery passes along the optic peduncle, and a short distance from the bulbus oculi divides into four or five branches. It sends two or three branches to the eye itself, and a reflex muscular branch into the MM. retractor bulbi and rectus posterior. The main portion of the artery turns dorsalwards and divides into three vessels:

(i) *R. muscularis*, which curls around the anterior aspect of the

optic peduncle and is distributed to the MM. rectus superior, anterior, and inferior.

(ii) *R. ophthalmicus superior posterior* (a.oph.s.p.). This branch passes directly dorsalwards and is distributed to the upper eyelid and the skin above the skull in the posterior orbital region, as well as to the tissue surrounding the eye itself. It fuses with the superior orbital branch of the A. petrosa lateralis.

(iii) *R. ophthalmicus superior anterior* (a.oph.s.a.). The third terminal branch of the ophthalmic artery passes dorsalwards together with the previous one and is distributed to the anterior portion of the upper eyelid and the skin of the head, as well as to the general tissues around the eye. It passes round the orbit along the dorsal border of the orbito-sphenoid and ultimately fuses with a branch of the palato-nasal artery and enters the nasal capsule. In addition it supplies both the oblique muscles of the eye.

5. Branches of the Systemic Arch (Pl. XIV).

The *systemic arch* runs in company with the carotid arch in an antero-dorsal direction to the occipital region of the skull, and then bends round mesially to unite with its fellow from the other side in the middle line to form the dorsal aorta (q.v.). The vessels given off from this arch are four in number.

A. A *cutaneous branch* passes dorso-laterally between the two portions of the M. cephalo-dorso-subpharyngeus to which it gives a small branch. It is distributed to the thymus and paratoid glands. This vessel arises very close indeed to the point where the 'third' arch enters the systemic, and in one specimen it appeared to be actually continuous with this vessel. In view of the fact that it divides the pharyngeal constrictor into two sections dorsally, just as the 'third' arch does ventrally, it would appear to be actually the peripheral continuation of this arch, but only an investigation of the conditions prevailing at the period of metamorphosis would settle this point.

B. *A. pharyngea ascendens* (Osawa) (a.ph.asc.).

A. maxillaris externa	Bethge (1898).
A. mandibulo-jugularis	Drüner (1904).

This artery arises laterally close to the previous one at about the level of the posterior end of the ceratohyal and passes antero-laterally, mesial to the M. depressor mandibulae, to the posterior edge of the squamosal. It has six branches:

(i) *RR. cutanei dorsales* (Osawa) of which one passes lateralwards

between the M. depressor mandibulae and the squamosal to the overlying skin and the anterior region of the paratoid, while the other passes posterior to the muscle and is distributed to the paratoid gland.

(ii) *R. hyomandibularis* (? *R. branchialis*, Osawa) (a.hym.) which passes lateralwards between the depressor muscle and the squamosal to the surface of the muscle, when it turns, coursing posteriorly across the muscle (in company with the N. jugularis—VIIth nerve), to its posterior edge. It then turns round anteriorly and mesially to be distributed to the dorsal surface of the M. interhyoideus posterior, while a further branch of this artery forks around the M. interhyoideus and is distributed to the posterior region of the lower jaw and the tissue directly mesial to it.

(iii) *R. mandibularis externus* (a.m.e.) which passes to the surface together with the previous branch, but then turns anteriorly and passes mesial to the jugal tendon, along which it sends a branch, while the remainder of the artery is distributed to the lateral surface of the lower jaw. It is a very small vessel, very much smaller than the artery of the same name in the Frog.

(iv) *R. pharyngeus* which passes postero-ventrally to the posterior end of the ceratohyal, and then loops forwards over the mouth-floor. This artery seems very variable in size and has not always been found.

(v) *R. mandibularis internus* which passes antero-ventrally to the mesial surface of the lower jaw. It is distributed to the skin of the ventral surface of the head, to the MM. intermandibularis and interhyoideus, passing right round the lower jaw to anastomose with its opposite fellow in the middle line and also with the ramus communicans of the sublingual artery (q.v.). It usually arises combined with the mandibularis externus for a greater or shorter distance.

(vi) A small *muscular* branch passing into the mesial surface of the depressor mandibulae.

It will be noticed that there is a striking resemblance between the distribution of the A. pharyngea ascendens, as described above, and that of the R. auricularis of the A. cutanea magna of the Frog, as described by Gaupp in his *Anatomie des Frosches*. The A. cutanea magna, however, is a branch of the pulmonary arch, while the A. pharyngea ascendens arises from the systemic arch. Nevertheless its origin is very close to the point where the ductus Botalli from the pulmonary enters the systemic arch. In the Frog there is no connexion between the pulmonary and systemic arches in the adult, but there is in the larva. In view of these facts, therefore, and bearing in mind that small cutaneous branches do actually arise from the ductus

Botalli in the Salamander, it seems not improbable that the A. cutanea magna of the Frog may be the morphological equivalent of the ductus Botalli+the A. pharyngea ascendens of Salamandra. The differences in detail between the branches of the A. pharyngea ascendens and those of the R. auricularis may easily be accounted for by the difference in the structure of the auditory organ in the two animals.

C. The *palato-nasal artery* (Pl. XIX, fig. 70) (a.pal.nas.) is, in the Salamander, a branch of the systemic arch. It arises dorsally close to the middle line, in the region of the occiput, and either close to, or jointly with the vertebral artery. Almost immediately it gives off a small twig to the dorsal wall of the pharynx, and then bends round laterally, following the curve of the systemic arch as far as the palatine foramen, when it turns sharply round mesially to the inner border of the orbit. At this bend four branches arise.

(i) *RR. pharyngei*, forming a rich network over the dorso-lateral pharyngeal wall. Usually two in number.

(ii) *R. pterygoideus* (a.pt.), a small branch passing along the pterygoid process of the palato-ptyergoid and shortly after, at a point ventral to the origin of the M. retractor bulbi a maxillo-palatine artery is given off.

(iii) *A. maxillo-palatina* (a.max.pal.), arising laterally and running in company with the maxillary vein. It is distributed to the roof of the mouth underlying the postero-lateral corner of the orbit and then turns anteriorly and is continued a short distance along the posterior region of the maxilla.

(iv) The *posterior palatine artery*, arising mesially and ramifying over the whole of the posterior region of the palate.

At the inner posterior angle of the orbit the palato-nasal artery turns anteriorly and gives off the anterior palatine artery and then continues forward as the orbito-nasal artery.

(v) The *anterior palatine artery* (a.pal.a.) also turns anteriorly and runs alongside the palatine vein and nerve supplying the mucous membrane of the middle and anterior regions of the roof of the mouth. The rich vascular network around the vomero-palatine teeth is also supplied by this artery.

(vi) The *orbito-nasal artery* must not be confused with the orbito-nasal of the Frog, which runs *dorsal* to the eye-muscles. It passes obliquely in an antero-dorsal direction across the surface of the orbito-sphenoid to the dorsal side of the inner anterior angle of the orbit, where it gives off a small twig, viz.:

(a) *R. descendens* which passes vertically downwards and spreads over the palate in that region.

The orbito-nasal artery then passes through a foramen in the processus antorbitalis, and divides into two terminal branches.

(b) A *mesial nasal* artery which immediately divides again into dorsal and ventral rami which bifurcate and spread around the mesial border of the nasal capsule.

(c) A *posterior nasal* artery (a.na.p.) which passes round the orbital border of the nasal capsule. Soon after its origin it gives off four twigs as under.

(1) The *anterior orbital* artery which passes backwards out of the same foramen as that by which the main artery (i.e. the orbito-nasal) entered. It is distributed to the pre-orbital glands of that region and also sends a branch to the overlying skin, and another which anastomoses with the dorsal branch of the ophthalmic artery, that is, with a branch of the internal carotid (see p. 201).

The posterior nasal artery then proceeds to the lateral border of the nasal capsule where it divides into the remaining three twigs.

(2) The *lateral nasal* artery (a.na.l.) which supplies the lateral border of the nasal capsule.

(3) The *mesial maxillary* artery (a.max.m.) which turns posteriorly and supplies the middle region of the upper jaw.

(4) The *anterior maxillary* artery (a.max.a.), turning anteriorly to supply the upper jaw in the region of the snout.

It will doubtless have been noticed that the vessel which has just been described as the palato-nasal artery bears a strong resemblance to one described by Gaupp for the Frog, and called by him the arteria occipitalis. Particularly is this so as regards its origin and its nasal branches. This agreement was considered by Bethge to be sufficiently close to justify his adopting the same name for the vessel in the Salamander, viz. arteria occipitalis. The A. occipitalis of the Frog, however, is a *dorsal* vessel, its orbito-nasal branch passing 'über den *M. rectus oculi superior*' (Gaupp), while in this animal also the palate is supplied by the *palatine artery* from the *internal carotid*. In view of these facts a non-committal name based on its distribution has been adopted here.

D. *Vertebral artery* (a.vert.) (*arteria vertebralis collateralis*, Bethge). It arises from the systemic arch close to, or together with, the palato-nasal artery just lateral to the occipital condyles, and, after running a short distance caudalwards, turns sharply in towards the vertebral column and then runs close alongside it posteriorly right down the body. It commences at about the level of the first vertebra, and

passes, ventral to the spinal nerves, through special foramina in the transverse processes of the ribs (see p. 19). Since the artery receives a number of reinforcements from the dorsal aorta (q.v.), which in the lumbar region are quite as strong or stronger than the original artery, it is probably more correct to regard the vessel as a series of segmental arteries which have fused with one another, rather than as a single vessel originating at the base of the skull. The latter view is, however, more convenient for descriptive purposes. A number of lateral vessels are given off to the muscles of the back.

(i) *Costal arteries* arise alongside or within the transverse processes of the vertebrae. In the latter case they soon emerge, after giving off a few small twigs to the Haversian canals of the bone, to run parallel with the ribs.

(ii) *Intercostal arteries* arise about midway between the previous ones, that is approximately opposite articulations between the vertebrae. They do not run directly lateralwards but in an oblique postero-lateral direction, the obliquity becoming more marked in the lumbar region. They are also distributed to the muscles of the back.

(iii) *Cutaneous* branches arise chiefly from the costal arteries and pass directly dorsalwards to supply the skin of the back, also giving a branch to the large cutaneous poison glands which occur along the mid-dorsal line. The capillary network forms a sort of vascular cup around the bases of these glands.

(iv) Occasional *anastomoses* with the *intraspinal* arterial system.

It must be observed that the arrangement of costal and intercostal vessels above described is not absolutely rigid. Many intermediate conditions are found, but on the whole these would seem to conform to a basic plan in which have been interpolated secondary additions.

In contradistinction to the Frog it should be noted that the vertebral artery is not responsible for the blood-supply to the *ventral* body-wall, since the epigastric artery (q.v.) discharges this function. The *arteriae abdominales* of the Frog are therefore not present in the Salamander as factors of the vertebral artery.

The vertebral artery also takes some share in the blood-supply of the anterior region of the oviduct, but, since these vessels usually arise from anastomoses with the dorsal aorta, they will be dealt with under the branches of the latter vessel together with the other oviducal arteries.

The Dorsal Aorta.

The *dorsal aorta* (d.a.) arises, as previously described, by the fusion of the paired systemic arches in the mid-dorsal line immediately

ventral to the base of the skull in the region of the occiput, that is some seven millimetres or so *anterior* to the origin of the subclavian arteries, and a very considerable distance before the mesenteric vessels are given off. The fusion of the aortic arches in the Salamander is thus much more complete than in the Frog and there is no question of any asymmetrical origin of the coeliaco-mesenteric vessels.

BRANCHES OF THE DORSAL AORTA

(Pl. XIV, fig. 61; and Pl. XVII, figs. 64 and 64a)

These may be arranged in three groups according to their distribution, as follows:

Group 1. Vessels of the Alimentary Canal (all of which leave the aorta in the mid-ventral line).

(i) *AA. gastricae anteriores* (a.g.a.) (Hyrtl, Osawa, Bethge). One or two small vessels arising at about the level of the subclavian arteries, and passing obliquely backwards through the mesentery to their distribution over the dorsal wall of the stomach.

(ii) A *coeliaco-mesenteric complex*, comprising one large vessel, which may be called the coeliaco-mesenteric artery, and a series of smaller ones arranged in 'anterior' and 'posterior' bundles.

The *coeliaco-mesenteric* artery (arteria intestinalis, Hochstetter) is a very large vessel almost equal to the diameter of that from which it springs. It arises at about the level of the tenth vertebra and opposite the posterior end of the stomach, immediately posterior to the junction of the post-caval and post-cardinal veins, and then passes ventrally through the mesentery to supply the stomach, spleen, pancreas, liver, duodenum, and the anterior section of the intestine, by means of the following four branches.

(a) *A. gastrico-lienalis* (a.g.lien.) or *A. gastrica posterior* (Hyrtl, Osawa) which, as its name implies, is distributed to the spleen and stomach. Its course runs anteriorly through the mesentery separating these two organs, more or less parallel with the vein of the same name, but nearer the stomach than the latter vessel. It supplies the dorsal stomach wall only, by means of a series of branches arising at intervals of about a millimetre along its length, and approximately at right angles to it. The spleen is supplied by a similar series of branches arising from the opposite side of the vessel.

(b) The *A. duodeno-hepatica* (a.d.h.) or *A. mesenterica prima* (Hyrtl, Osawa) which passes ventrally through the distal edge of the pancreas alongside the portal vein. Very soon after its origin one or two

branches arise which are distributed to the distal end of the duodenum, while a few small vessels pass into the pancreas from the main artery during its passage through the gland. The next important division of the vessel occurs about 5 or 6 mm. farther on when it bifurcates into *dorsal* and *ventral* hepatic arteries. The *dorsal hepatic* artery passes straight to the posterior end of the liver and then turns anteriorly along the dorsal surface of this organ on the right of the vein formed by the union of the abdominal and portal veins. Besides supplying the liver this vessel also sends branches to the ventral stomach wall, which pass along the mesentery together with the factors of the above-mentioned vein returning the blood from this section of the stomach-wall. There are usually two arterial branches to each venous factor. A small *cystic artery* to the gall-bladder also arises from this branch.

The *ventral hepatic* artery sends numerous branches to the duodenum in the region of the bile-duct, and then loops round the duct to enter the liver immediately ventral to it.

(c) The *A. duodeno-pancreatica* (a.d.pan.) or *A. mesenterica prima* (Hyrtl, Osawa) which passes through the pancreas proximal to the portal vein, and besides giving off considerable branches to the gland itself is distributed to the proximal region of the duodenum.

(d) The *mesenteric* branches (a.mes.a.) of the coeliaco-mesenteric artery which vary from two to four in number. They leave the artery posteriorly, the last one coming off very soon after its origin from the dorsal aorta, and are distributed to the proximal portion of the intestine.

After the large coeliaco-mesenteric vessel just described there arise from four to eight *anterior* mesenteric arteries (a.mes.a.) (*AA. mesenteriae accessoriae*—Osawa). These are given off serially from the section of the dorsal aorta corresponding approximately with the eleventh to the fourteenth vertebrae inclusive, and supply the distal portion of the intestine as far as the rectum, frequently spreading over the anterior end of this also. The interval between these vessels is only about a millimetre or a little more, and they tend to run obliquely forwards through the mesentery so as to be gathered together into a bundle just posterior to the coeliaco-mesenteric artery. They then bend back posteriorly to their distribution.

Distinguishable from the foregoing only by the fact that they arise after an interval of about 5 mm., and that they are not grouped quite so closely into a bundle, are about three *posterior* mesenteric arteries (a.mes.p.). They enter the dorsal side of the rectum. The interval between the origins of these vessels is rather greater than between

the anterior arteries above referred to. They are obviously equivalent to the AA. mesentericae posteriores of Osawa.

The distinction between anterior and posterior mesenteric arteries, as already indicated, must be largely arbitrary, the whole obviously forming a serial complex. It is for this reason that they have been regarded as regions of a 'coeliac-mesenteric complex'.

Group 2. Vessels of the Urino-genital System.

(i) *Ovarian* or *spermatic* arteries. The arteries to the gonads are essentially the same in both sexes. They consist of eight or ten fine vessels, i.e. four or five to either side, which arise mesially from the ventral side of the dorsal aorta and pass laterally towards their respective gonads through the mesovarium or mesorchium. Those of the right side are more anterior than the corresponding ones of the left owing to the asymmetry of the gonads, but in general they arise from the same section of the aorta as the anterior mesenteric vessels. They pass *mesially* to the kidneys, and tend to bifurcate very soon after their origin into two parallel but fairly widely separated vessels, which may occasionally bifurcate again. They frequently run in company with a factor of the post-caval vein. The *fat-bodies* are supplied by branches from these arteries.

(ii) The *renal* arteries (a.r.) (AA. renales—Osawa) consist of a number of extremely small vessels which arise from the aorta itself, from the oviducal, ovarian or spermatic arteries, or even from the dorso-lumbar arteries. At the posterior end of the kidney are a pair of much larger *superficial renal* arteries (a.r.s.) (A. suprarenalis—Osawa) which spread over the ventral face of the kidneys, their ultimate branches being connected with a number of small Malpighian bodies around the postero-lateral margin. The small deep renal arteries enter the kidney from the dorsal side.

(iii) The *uterine* or *oviducal* arteries. While these are essentially vessels of the female sex they are also present in the male, and are then distributed to the vestigial Müllerian ducts and ureters, so that they are strictly homologous in the two sexes. They are, however, very much smaller in the male than in the female. The following description is based on the conditions in the female. They arise in three regions, but are not entirely symmetrical on either side.

(a) The *posterior oviducal* arteries (a.od.3) arise from a common stem which leaves the dorsal aorta in the midventral line between the posterior lobes of the kidneys, just posterior to the left iliac artery. They are distributed to the expanded posterior end of the oviduct or 'uterus', passing along its ventral side and giving off numerous fine

branches which anastomose frequently, forming a fine vascular network, amounting almost to a 'rete mirabile'.

Besides giving off the posterior oviducal arteries their common stem also gives rise to one or both *superficial renal* arteries, and to a pair of *mesial cloacal* arteries (Figs. 64 and 64a) (a.cl.m.). These are essentially vessels of the male sex although also present in the female. In the male, these vessels, together with the superficial renal arteries, are the principal branches of the common stem, while the only vessels which may be considered the homologues of the oviducal branches of the female are two very small twigs arising from the superficial renals to the ureters and Müller's duct. In the female it is the cloacal branch which is vestigial.

In the male (Fig. 64a) after giving off the renal vessels, the cloacal artery proceeds dorso-posteriorly to the edge of the M. caudali-femoralis, to which it sends a branch, and it also gives a branch to the muscles of the back. The artery then turns sharply ventralwards along the anterior aspect of the cloacal gland, giving off two large branches which enter the gland mesially. A small continuation of the vessel finally anastomoses with a cloacal branch of the vesicular artery (q.v.).

The drawings (Figs. 64 and 64a) have been carefully made from a single specimen of each sex. Small individual variations from them may therefore be expected.

(b) The *middle oviducal* arteries (a.od.2) usually arise from the same section of the aorta as the posterior mesenteric vessels, but their exact point of origin varies considerably. They are usually asymmetrical, but either side may be the more anterior. From whatever level they may arise, however, they always run parallel with the aorta for a greater or shorter distance before turning lateralwards, dorsal to the kidneys, to pass via the mesentery to the oviduct at approximately the same level. Their branching commences within the mesentery before reaching the oviduct. Although they are vessels of considerable size they appear to supply only a comparatively short section of the latter organ, namely, just anterior to the vascular network of the posterior arteries. Renal arteries are given off by these vessels from the section which runs parallel with the dorsal aorta. It is probable that the posterior and middle oviducal arteries are together equivalent to Osawa's AA. uterinae.

(c) The *anterior oviducal* arteries (?A. oviductus—Osawa) (a.od.1) frequently arise in conjunction with a dorso-lumbar vessel, but they may come off independently from the dorsal aorta, or from the sub-clavian arteries, or even from the vertebral artery without any direct

connexion with the dorsal aorta. The anterior oviducal arteries are thus subject to a considerable amount of variation, and it is not possible to give a general description of them. The illustration (Fig. 64) shows one arrangement. It will be noticed that in this case the artery on the right side has no direct connexion with the dorsal aorta at all, but arises anteriorly from the vertebral artery, and posteriorly from one of the dorso-lumbar vessels which connect this artery with the dorsal aorta, while the artery on the left arises directly from the aorta posteriorly, and from a dorso-lumbar vessel anteriorly. In this case also each artery is in two sections, while in some specimens they are continuous. In one specimen, a female, they arose anteriorly from the *subclavian* arteries, and posteriorly from the dorsal aorta direct. They were continuous, and a connexion with the vertebral artery occurred at about the same level as the anterior origin of the vessels illustrated.

It will be noticed that they entwine the post-cardinal veins, and their association with these vessels is very close indeed, so that they are not easily distinguishable from them. It was doubtless the branches of these arteries that Rusconi mistook for factors of the post-cardinal veins, which led him to misname them the veins of the oviduct, and although Hochstetter was well aware of the true homology of the veins he also states that they receive numerous factors from the oviduct. Now while two or three factors do enter the post-cardinal veins from these organs they can hardly be described as numerous, and it is possible that Hochstetter too may have been confusing the arterial branches.

In the male these arteries are very small, and their branches form a fairly large-meshed regular network over the vestigial Müller's duct, giving a very pretty injection.

Group 3. Vessels distributed to the Limbs and Body-wall, &c. (Pl. XIV).

A. *A. subclavia* (a.scl.). The subclavian artery leaves the dorsal aorta at the level of vertebrae 3-4, and passes slightly obliquely towards the axilla. Its first branch is given off about 2 mm. from its origin.

(a) *A. thoracica* (Osawa) (a.th.). This vessel leaves the posterior aspect of the subclavian artery, passes dorsal to the fourth spinal nerve, and supplies the muscles of the body-wall immediately posterior to that nerve.

At the axilla there arises from the ventral aspect of the subclavian artery a short branch which almost immediately divides into the

A. epigastrica anterior and the *A. brachialis*. Dorsally there arise two smaller branches, the *A. subscapularis*, and the *A. circumflexa scapulae*.

(b) The *A. epigastrica anterior* (a.e.a.) (*A. cutanea magna*, Bethge) passes ventralwards round the body, deep to the *M. pectoralis*, but lateral to the longitudinal muscles of the ventral body-wall. At the lateral edge of the *M. rectus abdominalis superficialis* it turns abruptly caudad along the ventral parietes, between the *MM. rect. abd. super.* and *rect. abd. profundus*, and deep to the *M. obliquus externus*. It gives off branches segmentally at each muscular inscription, and unites finally with the *A. epigastrica posterior*—a branch of the iliac artery—thus forming a complete arterial loop along the ventro-lateral aspect of the trunk. Within the arm-pit the *A. epigas. antr.* gives the following two branches:

(i) *A. supracoracoidea* (a.sup.cor.) passing, with the nerve of the same name, over the dorsal surface of the coracoid, through the coracoid foramen, to supply the muscles arising from that bone. This branch is always small and is sometimes absent. In the latter case the muscles are supplied by a branch from the *A. pectoralis* which passes forwards over the posterior margin of the coracoid on its ventral aspect. The supracoracoid artery may apparently sometimes arise from the *A. subclavia direct*.

(ii) *A. pectoralis* (a.pect.). Leaves the anterior epigastric artery just before it turns caudad, and supplies the *M. pectoralis* and the skin covering it. One of its branches—which sometimes arises separately from the epigastric—turns anteriorly and enters the muscles covering the ventral surface of the coracoid.

(c) *A. circumflexa scapulae* (a.circ.sc.) arises dorsally from the subclavian artery and passes round the lateral face of the scapula in company with the *V. circumflexa scapulae*. It gives off the following six branches:

(i) *A. profunda brachii* (Osawa) (a.pf.br.). This artery enters the arm dorsally just posterior to the insertion of the *M. dorsalis humeralis*, and passes along the dorsal side of the humerus in company with the extensor nerves. It supplies the several heads of the *M. anconaeus* and the skin overlying it, and terminates finally in the skin within the bend of the elbow—*R. cutaneus brachii posterior* (Osawa).

(ii) *A. subscapularis* (Osawa) (a.s.sc.) passes round the mesial side of the scapula to the muscle of the same name.

(iii) and (iv) *RR. musculares* to the *MM. dorsalis humeralis* and *dorsalis scapulae*. These vessels enter the muscles mesially.

(v) *A. trapezia* (Osawa) (a.tr.) to the skin covering the anterior part of the shoulder and to the M. cucullaris.

(vi) *A. procoraco-humeralis* (Osawa) to the muscle of the same name and to the skin covering it.

(d) *A. brachialis* (a.br.) is the main artery of the fore-limb and forms the direct continuation of the subclavian artery. It enters the arm in company with the flexor nerves (N. brachialis). During its course through the arm it gives a branch to the M. humeri anti-brachialis inferior, and some of the ultimate twigs from this branch penetrate the muscle and supply the overlying skin. It varies somewhat as to its exact point of emergence from the main vessel—it may leave it at about the middle of the arm, or it may not emerge until near the elbow. In the latter case it runs backwards parallel with the A. brachialis before entering the muscle.

In the bend of the elbow the brachial artery gives off the *A. radialis* (Zuckermandl), which passes along the radial side of the fore-arm and first digit between the NN. cutaneus inferior lateralis and dorsalis manus radialis in company with the radial vein. From this artery, very close to its origin, arise several twigs to the skin, and a recurrent branch.

(i) *AA. cutanei antibrachii, medialis* and *lateralis* (Gaupp, Frog) with several branches supplying the skin on the posterior and flexor sides of the elbow. One branch, longer than the rest, extends down the flexor side of the fore-arm with the N. cutaneus brachii inferior lateralis.

(ii) *A. recurrens radialis*, a small vessel supplying the muscles on the flexor side of the elbow. Its name indicates the fact that it turns backwards in a proximal direction.

The direct continuation of the brachial artery is the *A. interossea* (Zuckermandl) or *A. mediana* (Osawa), from which arises the ulnar artery.

(i) *A. ulnaris* (Zuckermandl, Osawa). This artery and the one from which it arises correspond in course and distribution with the nerves of the same names. The ulnar artery remains on the flexor side of the M. interosseus and divides to supply the MM. flexor primordialialis communis, flexor antibrachii et carpi ulnaris, and the caput longum musculorum contrahentium. Immediately after its origin it gives a *R. recurrens ulnaris* which penetrates, and supplies, the muscles towards the extensor side of the elbow. A branch from it passes forwards superficially along the ulnar side of the limb to join

a second branch of the ulnar artery—*R. recurrens ulnaris anterior*—which leaves the A. ulnaris at about the middle of the fore-arm.

After giving off the ulnar artery the *A. interossea* passes to the extensor side of the M. interosseus. Immediately after doing so it gives off a branch which passes out at right angles, through the origin of the M. extensor antibrachii ulnaris, to the skin of the ulnar side of the elbow and fore-arm. It is the *A. collateralis ulnaris*, and its twigs fuse with those of the *R. recurrens ulnaris* and also with a terminal twig of the A. profunda brachii which probably represents the *R. collateralis radialis*.

At about the same level the A. interossea gives off a large branch which, after giving a small twig to the M. interosseus, turns dorsally and comes to lie immediately underneath the M. extensor digitorum communis. It is the second *main* branch of the interosseal artery.

(ii) The *A. interossea externa* (Zuckerkancl), or A. perforans superior (Osawa), spreads over the dorsum of the fore-arm and carpus, and supplies the extensor muscles. Three of its branches are worthy of note. First, the *R. recurrens posterior* passes backwards along the fore-arm and fuses with a branch—*R. collateralis posterior*—from the A. profunda brachii. The second passes over the carpus and supplies the M. abductor et extensor digiti I, and may finally unite with the A. perforans carpi. The third passes out to the skin on the ulnar side of the wrist and sends a branch to the ulnar side of the fourth digit, where it joins the *arcus dorsalis* from the A. perforans carpi.

The *A. interossea* proper passes along the fore-arm, just dorsal to the M. interosseus, without further branching. At the level of the ulnare + intermedium it divides, and the larger branch penetrates a foramen in this bone as the *A. perforans carpi* (q.v.), while the smaller continues the direction of the main vessel for a short distance and then spreads over the palm of the hand supplying the short flexor muscles of the digits—*A. volaris*.

The *A. perforans carpi*, after reaching the dorsal side of the hand, runs forwards to the level of the bases of the metacarpals, and then divides into two branches. Of these the pre-axial divides again so as to supply the adjoining sides of digits 1 and 2, and 2 and 3—the pre-axial side of the first digit being supplied by the radial artery. The post-axial branch of the A. perforans carpi divides to supply the adjoining sides of digits 3 and 4, and gives off a twig which crosses the base of the fourth digit to anastomose with a branch of the A. interossea externa and supply the post-axial side of that finger.

B. *AA. dorso-lumbales* (a.d-lum.). The dorso-lumbar arteries arise from the dorsal aorta at frequent intervals and pass directly dorsally to fuse with the vertebral arteries. In the anterior region of the trunk they are small, but increase in size and importance towards the sacral region. The anterior vessels take some share in supplying the anterior oviducal arteries (q.v.), while the posterior ones may give off small renal arteries to the kidneys, but with these exceptions their main function is to supply the muscles and skin of the back. Not infrequently a small dorso-lumbar artery may be found leaving the proximal portion of the common iliac artery (see also *A. vertebralis*, p. 204).

C. *A. iliaca communis* (a.il.com.). The *common iliac* artery leaves the dorsal aorta at the level of the sacral vertebra and passes across the dorsum of the pelvis to the leg. Its direction is slightly oblique in a posterior direction parallel with the transverse process of the vertebra and with the ilium. During its course it gives a small twig to the muscles of the back (see above). Just posterior to the hip-joint the common iliac artery breaks up into four branches. It is not easy to distinguish amongst them the familiar 'external' and 'internal' iliac arteries, but it would seem justifiable to regard the branch which passes antero-ventrally across the mesial face of the ilium as the *external iliac*, and the other three as representing together the *internal iliac*. These three branches are, the *A. vesicalis*, the *A. pudenda*, and the *A. ischiadica*.

(a) *A. iliaca externa* gives off its first branch almost immediately after separating from the iliac artery.

(i) The *A. glutea* (a.gl.) or (?) *A. femoralis* (Osawa) is a medium-sized vessel passing along the thigh antero-dorsal to the *A. ischiadica* and the sciatic nerve, and postero-dorsal to the femur. It supplies the MM. extensor ilio-tibialis and ilio-femoralis, and then continues down the thigh close to the femur to the knee. Here it gives off a *R. cutaneus cruralis posterior*, and then bends round the knee with the N. peroneus to join the R. recurrens of the *A. interossea externa*. It should be noted that the gluteal artery may sometimes leave the *A. iliaca communis* direct, from the angle between this vessel and the external iliac.

In the Frog the *A. glutea* is a branch of the *A. ischiadica* and is relatively much more limited in distribution, but it should be remembered that, in that animal, the *femoral* artery—i.e. the *pre-axial* vessel—is the main artery of the leg and the *A. ischiadica* is confined to the thigh, whereas in the Salamander the reverse is the case. The position of the *A. glutea posterior* to the hip-joint and *postero-dorsal*

to the femur excludes the possibility of any homology with the femoral artery such as Osawa's description seems to suggest.

(ii) The *A. obturatoria* (a.ob.) or *A. pelvica* (Osawa) is a small vessel arising from the external iliac at about the same level as the gluteal, or occasionally from a common stem with this vessel. It passes ventralwards over the dorsal surface of the pubo-ischium and supplies the origin of the M. pubo-ischio-femoralis internus, and, after passing through the obturator foramen, the origins of the muscles arising from the ventral face of the pubo-ischium, e.g. the MM. pubo-ischio-femoralis externus, pubo-ischio-tibialis, &c.

The external iliac then turns rather more ventrally and passes round the pelvis in company with the pelvic vein, crossing lateral to this vessel in the inguinal region. At the anterior border of the limb it gives off (iii) a small branch which enters the thigh between the MM. pubo-ischio-femoralis internus and extensor ilio-tibialis, and there divides into a branch supplying these muscles—particularly the former—and a cutaneous branch passing out to the skin—the *A. cutanea femoralis lateralis*. Although it is only small and comparatively insignificant the position and distribution of this vessel would suggest that it is to be regarded as the *A. femoralis*. The greater portion of the region characteristic of this artery is supplied by a circumflex and recurrent vessel from the *A. ischiadica* (q.v.).

(iv) The remaining portion of the external iliac is the *posterior epigastric* artery (a.e.p.), which, like its anterior counterpart, runs along the lateral body-wall at the level of the ventral border of the oblique muscles, just outside the peritoneum. It gives off segmentally *RR. abdominales* to the muscles of the body-wall, and finally anastomoses with the posterior extremity of the anterior epigastric artery so as to form a complete arterial loop along the side of the trunk (cf. p. 211).

(b) The *A. vesicalis* (a.ves.) passes ventro-mesialwards to the neck of the bladder, and care must be taken on stretching open the pelvis—after having split the pubic symphysis—to avoid rupturing the artery. On reaching the bladder it breaks up into a tuft of five or six small arteries, of which the majority supply the bladder, but one or two twigs spread over the ventral side of the rectum, while one branch passes back towards the cloaca and supplies the cloacal gland. This last branch sometimes fuses with the mesial cloacal artery.

(c) The *A. pudenda* (a.pud.) turns postero-ventrally and divides into two main branches, although other accessory twigs may occur. Of these one is a muscular branch and is distributed to the M.

ischio-femoralis and the ventral muscles of the tail—MM. caudali-pubo-ischio-tibialis and caudali-femoralis. The other branch is the *lateral cloacal artery* and is distributed to the gland, while a few twigs go to the skin at the base of the tail.

(d) The fourth and largest branch of the *A. iliaca communis* forms the direct continuation of that vessel, and is the *A. ischiadica*, or sciatic artery (a.is.). It enters the limb posterior to the acetabulum, and at first it is ventral to the corresponding vein, but within the thigh it twists round to the dorsal side.

(i) Its first branch is given off at about the middle of the thigh, and corresponds in position and distribution with the *A. profunda femoris* of the Frog, but it is a much smaller and less important vessel. Only a small portion of it is distributed to the M. ischio-flexorius, the major portion passing to the skin on the postero-mesial aspect of the thigh as the *A. cutanea femoris posterior* (Osawa) (*A. cut. fem. medialis*, Gaupp).

(ii) The most important branch of the *A. ischiadica* in the thigh is the *A. articularis genu tibialis* (Osawa). This vessel passes to the anterior aspect of the thigh round the ventral side of the distal end of the femur, and comes to lie between the MM. pubo-ischio-tibialis and pubo-ischio-femoralis. Here it breaks up into some four or five branches which supply the muscles named and the MM. pubo-tibialis and pubo-femoralis. Also there are one or two cutaneous branches which doubtless represent the *A. cutanea genu medialis superior* (Gaupp) of the Frog. Close to the origin of the *A. art. gen. tib.* a small twig arises for the M. femoro-fibularis. Two other branches are worthy of mention. The first of these is the *R. ascendens* (Osawa), a recurrent branch which passes back up the thigh and is distributed to the MM. pubo-ischio-femoralis internus and externus. Whether the twigs of this ramus anastomose with those of the *A. femoralis* is uncertain, but it is possible that they may. The second branch is the *R. descendens* (Osawa). This passes over the insertion of the M. pub. isch. tib. to the tibial side of the knee, and continues down the leg in company with the N. saphenus to the pre-axial side of the first digit. It supplies several cutaneous twigs to the extensor side of the leg.

(iii) Another branch arising from the *A. ischiadica* just proximal to the foregoing is the *A. articularis genu fibularis* (Osawa). This vessel leaves the sciatic artery postero-ventrally and supplies the *pars plantaris* of the M. ischio-flexorius and the insertion of the M. pub. isch. tib. as well as the skin on the posterior aspect of the thigh and knee.

The sciatic artery (*A. ischiadica*) now passes into the leg behind the knee and there divides into two terminal branches, viz. the *A. plantaris* (iv), a very short vessel which almost immediately divides into lateral and medial rami, and the *A. interossea* (v) which, like the nerve of the same name, passes to the extensor side of the leg.

The *R. plantaris lateralis* (Manno) passes to the tibial side of the leg, and sends a branch which becomes superficial at the lateral border of the insertion of the *pars plantaris* of the *M. ischio-flexorius*, and then gives off a *R. descendens* and a *R. ascendens*. The *R. descendens* passes down the leg to the sole of the foot, while the *R. ascendens* turns backwards to the lateral aspect of the knee and is distributed to the *pars plantaris* of the *M. ischio-flexorius* and to the insertion of the *M. pub. isch. tib.* The remainder of the *R. plantaris lateralis* continues down the leg on the mesial side of the tibia to the sole of the foot, and supplies the short flexor muscles of the tibial side. During its passage through the leg it gives a twig to the *M. pronator profundus* and to the *M. interosseus*.

The *R. plantaris medialis* (Manno) passes out to the fibular side of the leg, deep to the *M. flexor primordialis communis*, and immediately superficial to the *M. caput longum musculorum contrahentium*, in company with the *N. fibularis*. As it turns distalwards down the leg it gives a fairly large cutaneous branch to the flexor surface—*A. cutanea cruralis medialis* (Gaupp). It also supplies the muscles named above and then comes to lie—together with the accompanying nerve—close against the surface of the fibula. At the tarsus a cutaneous branch is given off to the skin on the fibular side of the ankle and a deep muscular branch to the *MM. flexores accessorii, medialis and lateralis*. It then continues along the fibular border of the tarsus to the base of the fifth metatarsal, where it turns mesially to supply the short flexor muscles of the fibular side of the foot.

(v) *A. interossea* (Zuckermandl).

A. perforans cruris (Manno).

A. tibialis medialis (Osawa).

Immediately after reaching the extensor side of the *M. interosseus* the interosseal artery gives off a superficial branch.

(va) *A. interossea externa* (O'Donoghue, in Sphenodon).

R. dorsalis cruris (Zuckermandl).

A. perforans superior (Osawa).

This artery supplies the skin on the dorsum of the leg—*A. cutanea cruralis lateralis*—and the extensor muscles. It lies on the tibial side of the *A. interossea* and is separated from it by the corresponding vein

and nerve. One noteworthy branch is the *R. recurrens* which runs back around the proximal end of the fibula close to the N. peroneus and anastomoses with the distal extremity of the gluteal artery.¹

The *A. interossea* proper passes right down the leg without branching, and, at the distal border of the *M. interosseus*, passes to the ventral side of the tarsus, and then, as the *A. perforans tarsi* (Manno) (*A. perforans inferior*, Osawa), penetrates to the dorsal side of the foot through the foramen between the tibiale and intermedium. Here it is known as the *A. dorsalis pedis* and divides into four branches, each of which divides again to form the *AA. digitales* supplying the adjoining sides of the toes.

6. Branches of the Pulmonary Arch (Pl. XXIII, fig. 77).

The *ventral oesophageal* (or pharyngeal) *artery* (a.oes.v.) arises mesially from the pulmonary arch at the posterior border of, and ventral to, the dilatator laryngis muscle. It passes anteriorly, dorsal to the *M. cephalo-dorso-subpharyngeus* and ramifies over the whole ventral surface of the pharynx and the floor of the mouth as far as the root of the tongue. Its most posterior branch is the *laryngeal artery* supplying the muscles of the larynx.

The *dorsal oesophageal* (or pharyngeal) *artery* (a.oes.d.) arises laterally from the pulmonary immediately opposite the ventral vessel, and bends dorsally round the oesophagus to meet a similar vessel from the opposite side, with which it fuses, and then continues as a median artery for some distance down the oesophagus posteriorly. These arteries thus form a Y-shaped vessel from which branches ramify over the whole of the dorsal surface of the oesophagus and pharynx.

The *pulmonary artery* (a.pul.), as the continuation of the arch may now be called, passes posteriorly, rather closely embedded in connective tissue, and enters the lung on its dorso-lateral border about a quarter of the way down. It commences to divide just before its entry into the lung.

Unless the small cutaneous branches of the ductus Botalli may be taken to correspond with the cutaneous artery of the Frog, this vessel is not represented in the Salamander (cf. pp. 202-3).

7. The Venous System.

The Venous Trunks (Pl. XV).

To be logical the course of the veins should be traced from their *distal* origins *towards* the heart, but, since it is impossible to see the

¹ The *A. interossea externa* may separate from the *A. ischiadica* before the *AA. interossea* and plantaris, the actual order of branching being somewhat indefinite.

smaller factors without the aid of a good dissecting microscope such as is not usually available to the ordinary student, the detailed description of the venous system is prefaced by the following short account of the sinus venosus and the main venous trunks entering it.

The *sinus venosus* forms a triangular swelling on the anterior end of the post-caval vein, almost directly after the latter emerges from the substance of the liver, on the left side of the heart. The base of the triangle is anterior. It may be seen from the ventral side, after opening the pericardium, by gently pressing back the left auricle. The ducts of Cuvier enter the basal angles, while the post-caval vein enters the apex.

The *left ductus Cuvieri* is either very short or entirely wanting, since the union of the post-cardinals with the anterior veins—the internal and external jugulars—occurs very close indeed to the sinus.

The *right ductus Cuvieri*, on the other hand, is quite long, and extends across the dorsal side of the heart—at about the level of the anterior end of the ventricle—since the union of the venous trunks on this side is symmetrical with that on the left, and occurs *outside* the pericardium. Thus a long ductus Cuvieri is necessary to reach the sinus venosus, which is situated well to the left of the middle line. It may easily be seen by turning the tip of the ventricle forwards.

The venous trunks uniting to form the ducts of Cuvier on either side are four in number, viz. the external jugular, the internal jugular, the subclavian, and the post-cardinal. The exact order in which these veins join up varies a little, but they may be easily identified as follows. The *external jugular* (v.j.e.) is the most anterior, and comprises (i) the *common facial* vein (v.f.c.) arriving laterally from the paratoid region, and (ii) the *lingual* and *thyroid* veins arriving from a mesial direction, the thyroid vein lying *ventral* and the lingual vein *dorsal* to the arterial arches. They unite to form a common vessel immediately posterior to the arches, and the vessel thus formed usually unites with the common facial vein to form a short trunk—the external jugular proper—which, in turn, joins the subclavian vein. It may, however, occasionally enter the subclavian separately from the facial vein.

The *subclavian vein* (v.scl.) is the largest and most prominent of the vessels entering the ductus, and also, with the exception of the thyroid vein, the most ventral, while its direction is almost exactly transverse, so that it is easily found and forms a useful landmark for identifying the other vessels.

The *internal jugular* (v.j.i.) arrives from an antero-dorsal direction and joins the subclavian vein close to the external jugular. It is most

easily found from the posterior aspect of the subclavian vein, between this vessel and the post-cardinal vein.

The *post-cardinal vein* (v.card.p.) lies very close to the oesophagus, round which it passes, and is the most posterior of the veins entering the ductus Cuvieri. It is only likely to be confused with the internal jugular, but it is more posterior than this vessel and more mesial, while its direction is slightly *postero*-dorsal as compared with the obliquely antero-dorsal direction of the internal jugular.

A rather tough connective tissue enclosing lymph spaces surrounds the whole of the venous complex just described, and, as the walls of the vessels are very thin, considerable care must be exercised in cleaning them to avoid rupture.

The ducts of Cuvier are often referred to as the pre-caval veins, but in view of the persistence of the post-cardinal veins in a functional condition, and the retention at the same time of their primitive connexions, it would seem preferable to call the vessel formed by the union of the post-cardinal vein with the derivative of the anterior cardinal vein (the internal jugular) the *ductus Cuvieri*.

8. Description of the Veins.

For descriptive purposes the venous system may be divided into groups according to distribution and function as follows:¹

Veins entering the Heart direct.

VEINS OF THE HEAD.

- A. Internal Jugular (see footnote).
- B. External Jugular.

VEINS OF THE TRUNK AND VISCERA.

- A. Post-caval.
- B. Post-cardinals.
- C. Subclavian.

VEINS OF THE LUNGS.

Veins of the Portal Systems.

HEPATIC PORTAL SYSTEM.

- A. Abdominal Vein.
- B. Portal Vein.

RENAL PORTAL SYSTEM.

- A. Caudal Vein.
- B. Common Iliac Veins.
- C. Pelvic Veins.

¹ The veins of the cranial cavity, factors of the internal jugular, are described at the end of the present section under 'Vessels of the Brain'.

Veins entering the Heart direct.

VEINS OF THE HEAD (Pl. XV and Pl. XIX, fig. 70).

A. *V. jugularis interna* (internal jugular vein) (v.j.i.). This important vein may be said to be formed by the fusion of two main factors. One of these lies *latero-dorsal* to the aortic arches and returns the blood from the occipital region and the muscles of the 'neck', and may be called the *V. jugularis lateralis* (v.j.l.). The other lies *ventro-mesial* to the internal carotid and the dorsal part of the systemic arch and drains the palate. This factor is the *V. pharyngo-palatina* (v.ph-p.) (Drüner). There are anastomoses between these two vessels that make it difficult to decide exactly which factors belong to each, and particularly is this so in the case of the *V. petrosa lateralis*, as it discharges into both vessels. It has been included among the factors of the *V. pharyngo-palatina*, as the contribution to this vessel is larger, and it also anastomoses with some of its palatine factors.

Owing to the large amount of individual variation met with, particularly in the palatine region, it is very difficult to give a detailed description of the factors of the veins of the head. Only the more constant features have been noted therefore, together with some indication of the types of variation to be expected.

Factors of the V. jugularis lateralis.

(a) *RR. musculares* from the MM. cucullaris and opercularis. These enter the vein variously as it passes along the ventral edge of the muscles.

(b) *V. occipitalis* (occipital vein). This vein arises just behind the head, between the MM. inter-transversarius capitis superior and inferior, by factors from these muscles and from the M. opercularis. It also receives:

(i) A small *V. post-occipitalis* from the cranial cavity, which passes through a foramen in the first vertebra, as in the Frog.

(ii) A *V. cranialis post-otica* (sinus jugularis, Rex) from the region of the medulla. This factor emerges from the cranial cavity together with the ninth and tenth cranial nerves.

(iii) A *R. muscularis* from the M. cucullaris, passing *dorsal* to the X+X ganglion.

(iv) An anastomosing factor from the vertebral vein.

The occipital vein joins the main vessel *ventral* to the IX+X ganglion.

(c) *V. vertebralis* (v.v.). The vertebral vein is one of the most

important factors of the *V. jugularis lateralis*. It collects the blood from muscles of the neck region on the dorsal side of the vertebral column. It passes anteriorly *dorsal* to the *M. opercularis* and the *Xth* nerve, and *mesial* to the *IXth* nerve to join the main vessel *posterior* to the *IX+X* ganglion.

Very frequently, but perhaps not quite constantly, the vertebral veins may be traced right through the dorsal muscles to the ventral side, appearing just anterior to the transverse process of the second vertebra. They then pass backwards alongside the vertebral column to join the post-cardinals at the point where they turn lateralwards to loop around the oesophagus. An anastomosis from the palatal region is also frequently received at the point where they emerge on the ventral surface of the muscles. The connexion with the post-cardinal veins is primitive, and in the Frog, where the post-cardinals are absent, the vertebral veins discharge entirely into the internal jugular veins.

(*d*) Another considerable tributary of the *V. jugularis lateralis* is an anastomosis with the *V. pharyngo-palatina*. It arises somewhat variously, either from the *V. pharyngo-palatina* itself, or from its mandibular factor, or even from the *V. petrosa lateralis*. It enters the *V. jugularis lateralis* ventrally just posterior to the columella.

(*e*) The only other tributary of note is the *dorsal branch of the V. petrosa lateralis*. This vessel leaves the *V. petrosa lateralis* within the antrum, and emerges between the columella and the processus oticus, looping round the *dorsal* side of the columella to enter the *V. jugularis lateralis* dorsally.

Factors of the V. pharyngo-palatina.

(*a*) *V. petrosa lateralis* (Drüner) (*v.pet.l.*).

<i>V. capitis lateralis</i>	Goodrich.
<i>V. lateralis</i>	Osawa.

This is the vessel which passes through the space between the palato-quadrate and the otic capsule—the antrum petrosum laterale. It drains the cranial cavity and the orbit by several factors as follows:

The *peri-orbital network* (*p.o.n.*) (see also Pl. XIII, fig. 58) is a wide venous girdle completely surrounding the bulbus oculi. It may be said to originate at the anterior border of the orbit where it receives the *V. nasalis* (*v.na.*) from within the nasal capsule, and a medium-sized cutaneous vein from the skin overlying it—*V. frontalis* (*v.fr.*). The network lies mainly, but not entirely, deep to the eye-muscles, and drains them as well as the tissues of the orbit generally. It is hardly possible to differentiate any particular vessel,

but one rather large vein, which may be termed the *V. orbito-nasalis* (v.o.na.) leaves the anterior end of the plexus and passes postero-mesially deep into the orbit to a point close to the optic fenestra, where it receives the *V. ophthalmica* (v.oph.) from the bulbus oculi. The ophthalmic vein passes inwards from the eye along the optic peduncle. The *V. orbito-nasalis* then turns dorsalwards and discharges into the posterior end of the peri-orbital network and more particularly into the *V. orbitalis superior*, (a factor of the *V. petrosa lateralis*), and into the superior facial vein (a factor of the *external jugular*).

The *V. orbitalis superior* (v.o.s.) lies deep to, and drains, the *M. levator mandibulae anterior* and the skin overlying it. It also drains the deeper parts of the dorsal portion of the peri-orbital network as already described.

The *V. orbitalis inferior* (v.o.i.) is the ventral counterpart of the above and drains the deeper regions of the peri-orbital network ventrally as well as a considerable portion of the levator bulbi muscle.

Another important tributary of the *V. petrosa lateralis* is the *V. anastomotica* (v.anas.) joining it to the palatal vessels. Sometimes it joins the *V. palatina* itself, more frequently the maxillo-palatine vein, and sometimes both vessels.

The *V. cranialis pro-otica* (Gaupp, in Frog) (v.cr.pr-ot.) or *V. cerebri anterior* (van Gelderen) is the chief vein draining the cranial cavity. It leaves the skull together with *N. ophthalmicus profundus* *V* and joins the *V. petrosa lateralis* mesially just as it enters the antrum.

Within the antrum a factor is received which enters the cavity between the *Proc. oticus* and the *Proc. ascendens*; the *V. petrosa lateralis* itself enters the antrum *ventral* to the *Proc. ascendens*, between it and the *Proc. basilaris*. It drains the *M. levator mandibulae*. Another small vein leaves the cranial cavity in company with the VIIth nerve and joins the *V. petrosa lateralis* near the posterior extremity of the antrum. It may be called the *V. cranialis mesotica* (v.cr.m-ot.) and obviously corresponds with the *V. cerebri medialis* of van Gelderen. At about the same level a small factor draining the loose connective tissue and skin immediately posterior to the ear can usually be found.

Van Gelderen has made a comparative study of the origin of the veins draining the cranium in vertebrates, and it is apparent, from his account, that the condition in *Salamandra* must be looked on as primitive.

(b) The factors from the palate entering the *V. pharyngo-palatina* are

extraordinarily variable. The whole region is highly vascular, and anastomoses are frequent, so that the several main vessels may vary considerably in size and extent from specimen to specimen or even on the two sides of the same individual.

The most mesial of them is the *V. palatina* (v.pal.). It arises by many fine tributaries from the region of the internal nares and from the mucous membrane covering the pre-vomer, and, following the curve of the posterior tooth-bearing process of this bone, drains the rich vascular network surrounding the bases of the teeth. Just in front of the dorsal portion of the systemic arch the palatine vein drains a venous plexus forming a coarse network on the roof of the pharynx in the middle region between the occiput and the posterior ends of the pre-vomerine teeth (pl.ph.). It then turns sharply laterally, and, following the curve of the systemic arch, joins the pharyngo-palatine vein at the side of the pharynx a short distance before this vein itself unites with the *V. jugularis lateralis* to form the internal jugular.

The vein just described lies mesial to the nerve and to the palato-nasal artery, but there is also a vein lateral to these structures which may accordingly be called the *lateral palatine vein* (v.pal.l.). It receives its blood from the mesial part of the floor of the orbit—from the *M. levator bulbi*, and the mucous membrane of the roof of the mouth—and may be distinguished from the *V. orbitalis inferior* in that it lies *ventral* to the *M. levator bulbi*. It nearly always joins the *V. anastomotica* of the *V. petrosa lateralis* and not infrequently the *V. palatina* also, but either of these connexions may be absent.

The *V. maxillo-palatina* (v.max.pal.) drains the anterior part of the upper jaw, and, at about the middle of the orbit, turns mesialwards and crosses obliquely towards the postero-mesial corner of the orbit. Here it may join the *V. anastomotica* and so empty itself into the *V. petrosa lateralis*, or it may pass somewhat more lateralwards and discharge into the *V. pharyngo-palatina direct*, while both connexions may be present. When it enters the *V. pharyngo-palatina direct* it does so close to the point where the *V. petrosa lateralis* and the *V. mandibularis profunda* are received.

The *V. mandibularis profunda* (v.m.pf.) arises from an anastomosis with the internal mandibular vein (a factor of the external jugular, q.v.) just posterior to the *N. intermandibularis*. It passes backwards, dorsal to the *MM. interhyoideus* and *interhyoideus posterior*, receiving blood from the former muscle, as well as numerous tributaries from the floor of the mouth between the lower jaw and the base of the tongue. Sometimes two vessels may enter the *V. pharyngo-pala-*

tina from the floor of the mouth, one from the mandibular region, and the other from the tissues on the dorsal side of the cerato-hyal, but this would appear to be merely a variety of the type where both regions drain into one vessel.

Close to the point where the above vessel is received a small *V. pterygoidea* (v.pt.) also enters. It arises in the posterior region of the upper jaw and passes backwards along the ventral side of the pterygoid.

B. The *external jugular* may be regarded as comprising three main venous factors:

(I) The *V. facialis communis* (v.f.c.), Vena jugularis externa (Drüner), or Vena jugularis interna? (Bethge). This vessel collects from three main regions, the orbit, the superficial intermandibular region, and the thymus. It arises in the orbit.

The *superior* and *inferior palpebral* veins (v.palp.s. and v.palp.i.) collect blood from the upper and lower eyelids respectively. These vessels unite at the posterior angle of the orbit where they are joined by several small factors from the glandular tissue of that region to form the superior facial vein.

(i) The *V. facialis superior* (v.f.s.) passes backwards superficially to the level of the thymus gland. It is closely applied to the skin, from which it receives numerous branches, particularly from the large paratoid gland of that region. In the region of the thymus it joins its ventral counterpart—the inferior facial vein.

(ii) The *V. facialis inferior* (v.f.i.) appears to arise at the tip of the lower jaw from the genio-glossus muscle, and from an anastomosis with the corresponding vessel of the opposite side, as the internal mandibular vein. The *V. mandibularis interna* (v.m.i.) passes through the loose connective tissue on the ventral side of the mandible. Numerous factors are received from the intermandibularis muscle and from the skin of the intermandibular region. At the posterior border of the muscle an anastomosis is received from the *V. mandibularis profunda*—a factor of the Internal Jugular—and from now on the vessel is spoken of as the *inferior facial vein* (v.f.i.). Continuing along the ventral surface of the mandible it passes dorsal to the M. interhyoideus and ventral to the M. interhyoideus posterior, receiving factors from both muscles. At the posterior angle of the lower jaw it turns abruptly dorsalwards to join the superior facial vein at the anterior border of the thymus as above described.

Numerous factors from the thymus gland enter the combined superior and inferior facial veins to form the common facial vein, which then proceeds ventro-mesially to enter the ductus Cuvieri as

already described. A small *laryngeal* vein can usually be found entering the vessel just before it merges into the ductus.

(II) The *V. lingualis* (v.ling.) or Vena pharyngea? (Bethge). This is essentially the vein of the tongue, emerging from that organ between the anterior and posterior radials of the copula, and running posteriorly along the mesial border of the first hypobranchial cartilage. At the point where the second hypobranchial cartilage unites with the first branchial arch the vein loops back on itself a little so as to allow it to stretch when the hyobranchial apparatus is protracted, while at this point also it receives a factor from the M. subarcualis rectus I. The vein then leaves the cartilage and turns somewhat mesially, passing *dorsal* to the arterial arches very close to their origin from the truncus arteriosus. As the vessel passes over the arteries it divides into two or more smaller veins which reunite to form a single vessel on the posterior side of the pulmonary arch, thus forming a closed venous loop. The reason for this is fairly obvious. The space between the arterial arches and the pharynx is very restricted, so that the vein must be subjected to considerable pressure both from the blood in the arteries and from food passing down the pharynx, and it is manifest that the blood would flow with more freedom under these circumstances if it were contained in several small vessels instead of in one large one. At this point also several large vessels from the ventral pharyngeal wall enter the vein, but the details are particularly difficult to determine owing to the fact that the blood or injection mass gets squeezed out of the veins by pressure from the arteries. Emerging on the posterior side of the arterial arches the vein turns sharply laterally and is soon joined by the thyroid vein, and sometimes also by the common facial before entering the *ductus Cuvieri*.

Just at the point where the lingual vein turns laterally to meet the thyroid vein it receives the efferent trunk from the central lymph heart, constituting one of the most important connexions between the lymphatic and venous systems. It is obviously this trunk which Drüner refers to as 'Vena reuniens' (see also p. 260).

(III) The *V. thyroidea* (v.th.) or *V. lingualis* (Bethge). The thyroid vein arises in the loose connective tissue between the hyobranchial muscles just anterior to the thyroid gland as the *V. thyroidea advehens* (Drüner) and passes posteriorly, ventral to the gland, receiving on its way numerous factors from the rich vascular network of the gland itself. At the posterior margin of the thyroid gland a *cutaneous factor* is received. This small vein arises in the skin in the neighbourhood of the gular fold and passes to the region of the os

triangulare in approximately the middle line. It then turns lateralwards, dorsal to the M. genio-hyoideus and ventral to the M. rectus cervicis to join the thyroid vein. It is very variable in size and extent.

After receiving the above-mentioned vessel the thyroid vein continues posteriorly as the V. revehens (Drüner), ventral to the aortic arches, to join the lingual vein. It occasionally unites with the facial vein just before this vessel joins the lingual.

It is not difficult to see how the system of the external jugular has been derived from the sinuses of the fish.¹ Thus the superior and inferior palpebral veins draining the peri-orbital network, and the superior and inferior facial veins appear to be derived, in part at least, from the orbital, post-orbital, and hyoidean sinuses of the Selachian, while the lingual and thyroid veins represent the inferior jugular sinus.

VEINS OF THE TRUNK AND VISCERA (Pls. XV and XXII).

A. The *post-caval* (v.c.p.) vein is a single, unpaired, more or less median vessel which first originates among the Dipnoi, and takes over the function of the post-cardinals by returning the blood from the posterior region of the body to the heart. It is general among the Amphibia and all higher groups. In the Salamander the transference of function is not complete, since the post-cardinal veins persist in the adult and are quite functional. In a few cases the post-caval may be wanting, with a consequent enlargement of one or other of the post-cardinal veins. These cases throw considerable light on the probable mode of origin of the post-caval, but the question will be reconsidered after giving a description of the vein as it is normally found in the adult Salamander.

The post-caval vein arises near the posterior end of the kidneys by the fusion in the middle line of a fairly large renal vein from either kidney. It continues anteriorly, ventral to the dorsal aorta, to the level of the coeliaco-mesenteric artery, receiving during its course numerous *renal* factors from the kidneys and two or three *genital* (spermatic or ovarian) factors from the *left* gonad and fat-body. The vein now divides: one half passes dorsally and almost immediately divides again as the post-cardinal veins, while the other, turning somewhat to the right, passes antero-ventrally into the liver as the true post-caval. The genital factors from the *right* gonad enter at about this point, either into the post-caval, or into the stem which is combined as the post-cardinals. The post-caval enters what appears to be

¹ Cf. O'Donoghue (1914).



a dorsal out-growth of the right lobe of the liver, the 'post-caval' lobe (Hohlvene Fortsatz, Hochstetter), which grows right down to the point where the post-cardinals are constituted and invests the vein very closely.

The post-caval becomes visible again on the ventral surface of the liver, just to the right of the gall-bladder, and it may be traced as a dark line passing obliquely across the liver to emerge free once more at the left edge of the pericardium, and, after a free course of about 6 mm., it enters the sinus venosus as already described. At the junction between the post-caval vein and the sinus venosus a pair of small veins enter, either together or separately. These have been called by Hyrtl the 'Venae abdominales anteriores', and Joseph for the sake of convenience adopts the same name. They are, however, the mesial branches of the *anterior epigastric* veins. They arise on either side by the bifurcation of the anterior epigastric veins into mesial and lateral factors (see under factors of subclavian vein, p. 230) at about the level of the posterior border of the coracoid. They pass mesially, dorsal to the rectus abdominis muscle, to unite and enter the sinus as described, or they may enter separately. The right anterior epigastric vein is necessarily longer than the left, and receives a factor in the middle line dorsal to the sternal plate. This small vein arises in the skin ventral to the sternum and passes either posterior to, or through the cartilage to reach the dorsal side. It would therefore seem best to call it simply the *sternal* vein.

If now the liver tissue be carefully teased away from that portion of the post-caval which passes through it, which is best done with blunt needles or seekers, numerous hepatic veins will be found entering it from the liver. They enter from both sides, but, on the left, there is usually one larger than the rest which is referred to as the *hepatic vein* (v.h.s.). Very occasionally this larger vein may enter on the right side.

We may now consider the cases where the post-caval vein is apparently wanting. There have been two such recorded, one by Hochstetter (1888), and the other by Joseph (1902), while Romeiser (1905) summarizes these two cases and describes a similar occurrence in *Necturus*. Both the cases mentioned are essentially similar except that in one it is the right, and in the other the left, post-cardinal that hypertrophies to carry the additional blood. An examination of the liver in these cases revealed a pair of exceptionally large right and left veins, more or less symmetrical, which fused near the anterior end of the liver, and then emerged from it as a single vessel to enter the sinus venosus in a precisely similar manner to the

normal post-caval. It would therefore appear that the post-caval vein is normally formed by a dorsal extension of the *right* hepatic vein anastomosing with the fused inter-renal portion of the post-cardinals. The dorsal extension of the right hepatic vein has been named by Hochstetter, who was the first to record the abnormality referred to, the 'Mittelstück' of the post-caval. The post-caval vein is to be regarded therefore rather as a modification of existing vessels than as a new structure.

B. The *post-cardinal* veins (v.card.p.).

Venae vertebrales	Funk.
Veines de l'oviducte	Rusconi.
Venae azygoi	Hochstetter.

In view of the above considerations the post-cardinal system should logically be regarded as arising from the posterior end of the kidneys as a median vessel, but since this section has already been included under the post-caval vein it will be described from the point where the post-cardinal veins separate from the latter vessel.

As already mentioned, the post-cardinal system separates from the post-caval as a single vessel which almost immediately divides into two, and these pass anteriorly on either side of the dorsal aorta. One case has been found in which the right post-cardinal passed dorsal to the aorta to reach the right side, but this is abnormal, the veins usually remaining ventral to the artery. This division takes place at the anterior end of the kidneys, and occasionally a remnant of the primitive connexion between the post-cardinals and Jacobson's vein may persist.

During their course alongside the aorta the post-cardinal veins receive tributaries from the muscles of the back. These join the main veins at about the centre of each vertebra and appear at first sight to enter alternately from the right and left sides, but on closer inspection each tributary is found to collect from both sides. The tributary from the side opposite to that of the main factor passes ventrally between the muscle and the vertebra, and then crosses over the middle of the vertebra and dips dorsalwards again between the vertebra and the muscle on the other side to join the main factor within the substance of the muscle. A little dissection is therefore necessary to display the relations. Besides these dorsal factors the post-cardinal veins also receive some three or four *anterior oviducal* veins from the anterior portion of the oviduct connecting them with the *longitudinal oviducal* vein (v.od.long.). This vessel runs along the ventral aspect of the anterior three-quarters of the oviduct (i.e. along the portion

anterior to that in which the embryos develop), draining the whole of the blood therefrom and delivering it, by means of the anterior oviducal veins above mentioned, into the post-cardinal veins. The anterior oviducal veins are somewhat variable in number and position and should be distinguished from the anterior oviducal arteries (see p. 209).

Hochstetter (1888) figures the right post-cardinal passing dorsal, and the left ventral to the corresponding subclavian artery. While this arrangement is not infrequent it would appear normal for both veins to pass dorsal to the artery.

Just before the veins cross the arteries they receive an anastomosis from the post-axial vein of the arm. This vessel, usually quite small, runs parallel with, and posterior to, the subclavian artery. It would appear to be an enlarged parietal vessel (see also p. 234).

Immediately anterior to the subclavian arteries the post-cardinal veins turn off laterally at right angles to loop around the oesophagus. At this point a number of fine vessels enter, including one of variable size which continues the direction of the post-cardinals along the remainder of the vertebral column as far as the occiput, where it usually anastomoses with the vessels of the pharyngeal plexus. It is also in communication dorsalwards with a factor of the internal jugular within the substance of the muscles (see p. 222). Osawa (1902) calls this vessel the anterior cardinal vein, but since the internal jugular must be regarded as the derivative of that sinus, the anterior prolongation of the post-cardinal vein is here called the *vertebral vein*.

The origin and development of the post-cardinal veins, their relation to the kidneys and to Jacobson's veins, were first described by Hochstetter (1888) for *Salamandra atra*. The substance of his work is quite well known and there is therefore no need to repeat it here.

C. *V. subclavia* (v.scl.) or *V. cutanea magna* (partim) (Bethge). In addition to the blood from the fore-limb the subclavian vein also receives two important factors from the muscles and skin of the trunk, viz. the *V. lateralis* and the *V. epigastrica anterior*. The description of the subclavian vein thus falls naturally into three heads.

(a) *V. epigastrica anterior* (v.e.a.). The anterior epigastric veins lie in the ventral body-wall alongside the arteries of the same name, at the lateral edges of the MM. recti abdominales superficiales. Each arises a little posterior to the caudal edges of the liver by factors from the neighbouring muscles, as well as by transverse tributaries from the median epigastric vein (see p. 237), and passes forwards to the posterior border of the coracoid, where it divides into two branches.

The *mesial* branch of the *left* side continues directly forwards, inclined slightly mesiad, and enters the junction of the post-caval and sinus venosus. The *mesial* branch of the *right* side also passes forwards to the pericardial margin and then turns abruptly to the left around the apex of the pericardium and joins its fellow on the left side just as it enters the post-caval. The *lateral* branches of the anterior epigastric veins are symmetrical, so that the description of one will serve for both. It accompanies the artery and turns sharply dorsally to the region of the axilla, where it joins the V. *lateralis* and the V. *brachialis medialis*. On its way it receives two important factors:

(i) *V. pectoralis* (v.pect.) from the muscle of the same name, as well as from the M. coraco-brachialis brevis. The factor from the latter can be traced right down the muscle into the arm, where it appears to form a direct continuation of the V. *anastomotica brachii* (see also p. 235).

(ii) One or two *VV. cutaneae* from the skin of the axilla.

The exact pattern of the junction of the vessel with the V. *lateralis* and V. *brachialis medialis* is somewhat variable, but usually the V. *lateralis* and anterior epigastric vein first join to form a short common trunk, a *V. axillaris* (v.ax.), and then receive the vein from the arm.

The vessel just described is called *the* epigastric vein in *Cryptobranchus* (Osawa) and *Rana* (Gaupp).¹ In the Salamander it is normally larger than the *mesial* branch of the anterior epigastric vein and therefore carries most of the blood from that vessel. Nevertheless it seems quite probable that it actually represents a 'V. coraco-pectoralis' which should be regarded as a factor of the V. *axillaris* that has become secondarily associated with the V. *epigastrica anterior* by fusion with a factor of the latter vein, the association becoming increasingly stronger during phylogeny until it finally provides the only path of egress for the blood from the epigastric vein. Such an hypothesis is rendered the more probable in that it allows a simple explanation of the direct connexion between the anterior epigastric veins and the sinus venosus in Salamander, which would otherwise be somewhat puzzling.

As is well known from the work of Goette, Hochstetter, and others, the abdominal vein in *Amphibia* develops by the fusion of a pair of lateral vessels connected anteriorly with the sinus venosus or ductus Cuvieri and posteriorly with the iliac veins. In the Frog the former connexion normally disappears while the latter develops

¹ In these animals there is no connexion between the anterior epigastric vein and the sinus venosus, although it is possible that one may exist in *Cryptobranchus* but has been overlooked by Osawa. It is very easily destroyed in opening the animal.

as the pelvic veins. The Dipnoi also possess an abdominal vein, but in these animals the anterior connexion is also retained. Now in *Salamandra* the anterior epigastric veins are connected by a short common stem with the sinus venosus post-caval junction, and posteriorly with the abdominal vein, by means of the median epigastric. It seems therefore not unreasonable to suppose that they represent the primitive vessels connecting the abdominal vein with the sinus venosus, a connexion which is in the process of being replaced by the lateral connexions with the VV. axillares, while their anterior junction with the heart has become secondarily associated with the posterior end of the sinus venosus rather than with the ductus Cuvieri.

(b) *V. lateralis* (v.l.) or *V. cutanea magna* (partim) (Bethge). The two synonyms for this vessel are fairly uniformly distributed throughout the literature, but the former has been chosen as it is not by any means a purely cutaneous vein, but receives numerous factors from the muscles of the body-wall also. It was first described by Bethge in 1898.

The lateral vein arises at the side of the tail, a little posterior to the cloaca, immediately beneath the skin, and passes right along the body in the sulcus lateralis between the dorsal and ventral body-muscles to a point just anterior to the third myoseptum. On its way it drains both the skin and the muscles of the lateral body-wall. An important anastomosis with the *V. iliaca transversa* occurs in the pelvic region (see p. 243), and sometimes one with the *V. pelvica* also. It is in communication with the lymphatic system by means of the lateral lymph hearts which occur at each myoseptum (see also pp. 253, 259). The vessel has a tendency to sink into the sulcus lateralis and to become partly hidden by the muscles. At the anterior end it passes inwards, deep to the *M. dorsalis humeralis*, and then turns sharply ventralwards just anterior to the third rib, passing deep to the portion of the *M. thoraci-scapularis* arising therefrom. At this point a vessel is received from the *M. thoraci-scapularis* and the anterior body-muscles beneath the supra-scapula. This portion of the vein is called the cervical portion of the *V. cutanea magna* by Osawa, but since it has no connexion with the skin, and is a purely muscular vein, it would seem to be a misnomer. At the posterior border of the glenoid cavity it is joined by a cutaneous vein from the skin covering the *M. dorsalis humeralis*, the *V. cutanea dorsalis scapulae posterior* (v.cut.d. sc.p.) and then almost immediately unites with the lateral branch of the *V. epigastrica* anterior to form the *V. axillaris* (v.ax.). At this point an anastomosis with the *V. brachialis medialis* may occur, but is not constant. At the posterior border of the scapula the *V. dorsalis*

scapulae is received from the MM. *dorsalis scapulae* and *dorsalis humeralis*, and at about the same point a large branch from the V. *brachialis medialis* as well as the V. *cutanea humeri posterior* from the M. *anconaeus* and the skin covering it. The vessel, which may now be called the V. *circumflexa scapulae* (v.circ.sc.), passes lateral to the ventral end of the scapula, between this bone and the muscles covering it, and dorsal to the head of the humerus. At the anterior border of the scapula the V. *brachialis lateralis* joins the vessel, as well as small factors from the MM. *cucullaris* and *opercularis* and also a larger cutaneous vein, the V. *cutanea dorsalis scapulae anterior* (v.cut.d.sc.a.) which latter drains the skin covering the M. *dorsalis scapulae*.

The subclavian vein (v.scl.), as it may now be called, continues directly forwards along the dorso-lateral margin of the procoracoid, and, near the anterior extremity thereof, receives the V. *supracoracoidea* (v.sup.cor.). This factor drains the muscles of the same name, and then penetrates the coracoid foramen and crosses the dorsal surface of the procoracoid almost at right angles to its long axis. After receiving the supracoracoid vein, the subclavian turns in mesially and joins the internal and external jugulars and post-cardinal to form the ductus Cuvieri.

There is a small vessel joining the anterior aspect of the subclavian vein just before it enters the ductus Cuvieri which Bethge calls the V. *cutanea parva* (v.cut.pa.). It collects from the posterior margin of the thymus gland, and from the overlying skin, and it also receives some small twigs from the M. *cucullaris*. The hypoglossal nerve passes between this vein and the V. subclavia, and thus forms a useful landmark for identifying the vein.

(c) *Veins of the Fore-limb.* These arise between the fingers as the *VV. interdigitales* which flow into a venous arc stretching across the dorsal surface of the hand at about the level of the centre of the metacarpals—the *Arcus venosus dorsalis manus* (Osawa). On the radial side of the limb this arc flows into the V. *superficialis radialis* (Osawa), and at about the same point a large palmar cutaneous vein enters. The V. *superficialis radialis* continues along the fore-arm, just under the skin, between the flexor and extensor muscles of the radial side. It drains the muscles by several large twigs, and, at the elbow, it receives a large R. *communicans* from the V. *interossea*. From this point to the shoulder the vessel becomes the V. *brachialis lateralis* (Osawa). It receives, just proximal to the elbow, one or two large cutaneous factors, as well as several twigs from the adjoining muscles. At the proximal end of the arm, quite close to the shoulder, there is yet another deep plexus, lying on the flexor side of the humerus,

whereby communication is established between the lateral and medial brachial veins as well as with the *V. anastomotica brachii*. Directly anterior to the insertion of the *M. procoraco-humeralis* the *V. brachialis lateralis* joins the *V. circumflexa scapulae* to form the *V. subclavia* as described above.

The *V. interossea* arises on the dorsum of the hand by several factors from the ulnar and middle regions of the *arcus venosus dorsalis manus*, and from the several extensor muscles of that region. These factors unite to form a single vessel at the proximal border of the carpus, just mesial to the distal end of the ulna, and pass along the fore-arm on the extensor side of the *M. interosseus* in company with the artery and nerves. At the proximal end of the muscle it passes to the flexor side of the limb and receives a large factor—the *V. antibrachii ulnaris*—draining the flexor muscles of the ulnar side of the limb, as well as the *M. flexor primordialis communis*, the *MM. flex. accessorius medialis* and *lateralis*, and the *M. pronator profundus*. It may also anastomose with the palmar factor of the *V. super. radialis*, but it is uncertain whether this is constant.

At the flexor side of the elbow the combined vein divides into three. Of the two main limbs one fuses with the *V. brachialis lateralis*, the other becomes the *V. brachialis medialis* (*v.br.m.*) and passes along the ventral, or mesial side of the arm. The third branch, much smaller than the other two, is the *V. anastomotica brachii*. Not infrequently the *V. brachialis medialis* and the *V. anastomotica brachii* arise as a single vessel and divide later.

As the *V. brachialis medialis* becomes superficial it receives one or two large cutaneous veins—*VV. cutaneae antibrachii mediales*—from the skin covering the ulnar side of the fore-arm. It also drains both the extensor and flexor muscles of the arm. Near the shoulder it receives a fairly large factor whereby it communicates, through the plexus above mentioned, with the *V. brachialis lateralis* and *V. anastomotica*. It then turns somewhat posteriorly, and, after receiving another factor from the skin of the arm, it joins, or sends a large branch to, the *V. axillaris*. In the latter case the remaining portion passes antero-mesially beneath the scapula, ventral to the nerves of the brachial plexus, and, after receiving a small twig or two from the *M. thoraci-scapularis*, enters the post-cardinal vein close to the point where it bends around the oesophagus. If the whole of the *V. brachialis medialis* joins the axillary vein then a branch from the common vessel thus formed passes to the post-cardinal. The relations in this region are subject to a considerable amount of variation, and, in one case, the vessel passing to the post-cardinal was so fine as to be almost

non-existent, but a larger vessel, leaving the V. axillaris at about the same point, passed anteriorly, ventral to the nerves, and entered the subclavian vein anterior to the shoulder. Grodziński (1930) states that the vessels supplying the developing fore-limb in *Amblystoma* form a network just proximal to the glenoid region, from which the subclavian and other veins develop by the enlargement of some vessels at the expense of others, so that the network ultimately disappears. Assuming that the development of *Salamandra* follows similar lines, it is easy to understand the rather considerable variations in the connexions just described.

The *V. anastomotica brachii* (v.anas.br.) has already been mentioned several times. It is a curious little vessel which arises in the plexus just proximal to the elbow and passes up the flexor side of the arm between the two main veins. It passes right across the ventral side of the shoulder-joint and penetrates the M. coraco-brachialis brevis to join the V. pectoralis (cf. p. 231). It drains the muscles alongside which it passes, and communicates with the other two brachial veins at the plexus just distal to the shoulder, as already described.

It should be noted that the vessel which Bethge calls the 'Vena cutanea magna' comprises those here described under V. lateralis, V. axillaris, V. circumflexa scapulae, and V. subclavia.

VEINS OF THE LUNGS.

The *pulmonary veins* arise on the mesial aspect of the lungs and pass transversely from the proximal ends of those organs across the ventral wall of the oesophagus, where they fuse, near the middle line, to form a single unpaired vessel which runs directly forwards and enters the left auricle of the heart. The junction of the right and left pulmonary veins occurs immediately dorsal to the apex of the ventricle.

A few small factors from the ventral oesophageal wall also enter the pulmonary veins. As the pulmonary vein passes between the oesophagus and the sinus venosus it becomes embedded in the tissues of the dorsal wall of the latter. Its entry into the left auricle is not valved (see also p. 188).

Veins of the Portal Systems

THE HEPATIC PORTAL SYSTEM (Pl. XXII).

A. *V. abdominalis* (v.abd.) (Hochstetter) (see also Pl. XVI). An abdominal vein is present as in the Frog, but instead of being formed largely by the fusion of the two pelvic veins, as in that animal, it

also receives the considerable addition of the following two median veins in the pelvic region.

(a) The *median cloacal vein* (v.cl.m.) arises from the anterior and mesial regions of the cloaca by several fine factors and runs forwards in the middle line ventrally, along the pubo-ischiadic symphysis, immediately under the skin. At the ypsiloid cartilage it bends round, either to the right or left, and joins the abdominal vein in the middle line at its formation by the fusion of the right and left pelvic veins.

(b) The *posterior vesical vein* (Fig. 63; v.ves.p.) enters the abdominal at the same point, but lies *dorsal* to the pubo-ischiadic symphysis. It drains the blood from a rich vascular network spread over the posterior region of the bladder, and receives a pair of veins from the dorsal side of the pubo-ischium. These small factors are readily broken when the pubo-ischiadic symphysis is split and pulled apart, so that they are easily overlooked. They receive a small tributary which passes through the obturator foramen from the ventral side.

The abdominal vein passes forwards in the middle line from the anterior edge of the pubes to the anterior extremity of the bladder (about 14 mm.) through the subperitoneal epithelium, without receiving any further factor of importance other than a small *ypsiloid vein* at the anterior end of the ypsiloid cartilage from the surrounding tissues and skin of that region.

At the anterior end of the bladder it is joined by vessels from this organ.

(c) One or more *anterior vesical veins* (Fig. 63; v.ves.a.) collecting the blood from the anterior, ventral, and lateral regions of the bladder.

(d) The *vesico-haemorrhoidal vein* (v.ves.hm.) comprising two main factors.

(i) A *dorsal vesical vein* formed by many factors from the dorsal bladder-wall. These usually unite to form a single vessel before joining the other factor, but may enter at several points.

(ii) A *ventral rectal vein*. It is important to notice that the whole of this vessel lies *ventral* to the gut, i.e. between it and the bladder. The blood from the *dorsal* side of the rectum enters the portal vein by means of the haemorrhoidal vein, but there appear to be frequent fusions within the tissue of the rectum between the factors of these two vessels.

The combined dorsal vesical and ventral rectal veins form the vesico-haemorrhoidal vein which enters the abdominal a little anterior to the bladder.

In one case the abdominal vein divided at this point to reunite a little farther on, forming a closed loop. Normally, however, it con-

tinues undivided to the liver. It passes dorsal to this organ, and about 5 mm. from its edge, fuses with the anterior gastric branch of the portal vein, which, continuing along the dorsal side of the liver, appears to be a direct continuation of the abdominal vein. The section between the anterior end of the bladder and the posterior edge of the liver receives some two or three tributaries.

(e) Several factors from the ventral body-wall and the rectus abdominis muscle. These factors frequently, if not invariably, anastomose with factors of the *anterior epigastric veins*. They often, instead of entering the abdominal vein direct, enter the median epigastric vein (see below) to which they probably belong.

(f) A small factor from the proximal end of the duodenum may frequently be found entering the ventral side of the abdominal vein at the point where it crosses that section of the gut.

(g) The *median epigastric vein* (v.e.m.) is represented by one or two factors of the abdominal vein lying ventral to it and collecting from the ventral parietes. It corresponds very closely with the similarly named vein in Reptiles as described by Beddard (1906) and O'Donoghue (1921).

The epigastric veins are notoriously difficult to investigate, and the Salamander is no exception. So far as could be determined the median epigastric vein extends anteriorly through the subperitoneal epithelium as far as the sternal cartilage. Whether it anastomoses with the sternal vein could not be determined with certainty, since the pressure of the cartilage squeezed all the injection fluid and blood from this section. In any case if such a connexion exists it is very small. The vein receives several lateral factors which in some cases appear to anastomose with corresponding factors of the anterior epigastric veins. They correspond roughly in number and position with the inscriptions in the rectus abdominis muscle. (For relations of the anterior epigastric veins see pp. 230, et seq.) A comparison with the work of Beddard and O'Donoghue will readily demonstrate the striking general agreement between the abdominal, pelvic, and epigastric veins of the Salamander and the reptiles concerned, particularly *Sphenodon*, a fact which has also been noted by O'Donoghue in his account of the vascular system of this animal.

B. The *V. porta* (v.p.) arises dorsally at the level of the pylorus (i.e. at about the middle of the body cavity) by the junction of the lieno-gastric vein with the mesenteric veins. It runs in a dorso-ventral direction, slightly obliquely anteriorly, passing through the pancreas a little posterior to the hepatic artery.

It should be noted that the factors and branches of the portal vein

pass through the mesentery on the *left* side, and the branches of the mesenteric arteries on the *right*.

The factors of the portal vein.

(a) The *V. gastrico-lienalis* (v.g.lien.) runs posteriorly through the mesentery which suspends the spleen from the dorsal stomach-wall. It is constituted by a series of tributaries, on the one side from the gland, and on the other from the dorsal stomach-wall, and is the venous counterpart of the lieno-gastric artery which runs more or less parallel with the vein, between it and the stomach.

Just before its junction with the mesenteric veins it gives off a small branch which may be termed the *minor portal vein*. This vessel passes along the postero-ventral side of the post-caval lobe of the liver.

As was the case with the arterial system it is not easy to differentiate the anterior from the posterior mesenteric vessels. The following arrangement seems to be the most satisfactory and convenient generally.

(b) The *V. haemorrhoidalis* (v.hm.) drains the blood from the dorsal side of the rectum, and the extreme posterior end of the intestine. A short distance before it unites with the lieno-gastric vein at the origin of the portal vein it is frequently joined by the posterior intestinal vein.

(c) The *V. intestinalis posterior* (v.in.p.) is the largest of the three intestinal veins. It returns the blood from the posterior two-thirds of the intestine (excluding the rectum). It always enters the portal vein in very close association with the haemorrhoidal vein, and as already stated they frequently unite and enter as a single vessel.

(d) and (e) *The middle and anterior intestinal veins*. These two factors enter the portal vein at intervals of about a millimetre along its length. Their origin in the intestine is very restricted, and together they return the blood from the remaining third of the intestine and the posterior end of the duodenum. There is much variation.

(f) *Rusconi's vein* (v.R.) (Hochstetter), or *V. omphalo-mesenterica sinistra* (Choronshitzky). This vessel arises from numerous factors in the duodenum and anterior part of the intestine, and passes cephalad, parallel with the gut, to about the middle of the duodenum, where it turns dorsalwards and enters the pancreas to join the *pancreatic vein*, the common trunk thus formed finally uniting with the portal vein just before this vessel joins the abdominal vein.

The vessel under consideration was first described by Rusconi, who referred to it as the longitudinal vein of the gut, while its onto-

genetic history has been investigated by Choronshtitzky (1900), who showed that it is really the persisting left *vitelline* vein of the embryo. It is therefore homologous with the V. subintestinalis of the fish. According to this author the right vitelline vein is never large and disappears early. Hochstetter (1908) confirms these views.

(g) The *anterior gastric vein*.¹ It would perhaps seem more correct to regard this vessel as a *branch* of the portal vein than as a *factor*, but actually it is both. It passes along the dorsal surface of the liver and has the appearance of being the direct continuation of the abdominal vein. On the one side it sends numerous branches into the liver, and on the other it receives four or five factors from the ventral stomach-wall. These factors are always associated with corresponding arteries, and there is usually an artery on either side of the venous factor.

It should be noted that the blood-system of the stomach is of a two-fold nature. It both receives its blood from, and returns it into, distinct vessels on both dorsal and ventral sides.

THE RENAL PORTAL SYSTEM (Pl. XVI).

A. The *V. caudalis* (v.cd.), as its name implies, arises near the extremity of the tail and runs forwards through the haemal arches ventral to the caudal artery. Almost immediately after it emerges from the haemal canal it divides symmetrically into two vessels, which pass respectively to the dorso-lateral border of each kidney. These veins are portal to the kidneys. Hochstetter's name for them is retained, namely, Jacobson's veins.

VV. Jacobsoni (v.J.) (Hochstetter). Each Jacobson's vein, almost immediately after its origin from the caudal vein, receives a small *inguinal* vein from the muscles of the inguinal region, and then passes to the dorso-lateral surface of the kidney, to which organ it gives a number of *Venae advehentes*. Just before reaching the level of the iliac artery Jacobson's vein bends round the edge of the kidney to the ventral side, passes ventral to the artery, and immediately anterior to it anastomoses with the common iliac vein. Jacobson's vein, thus reinforced, passes anteriorly along the lateral border of the kidney, giving off on the one side numerous *Venae advehentes* to the kidney, and receiving on the other four or five *dorso-lumbar* veins from the muscles of the back, and also a number of posterior

¹ This terminology is due to O'Donoghue (1921). Beddard (1905) regards it as the anterior continuation of the abdominal vein. As O'Donoghue rightly points out, only a study of its development can decide to which it belongs. Reference should be made to O'Donoghue's paper.

oviducal veins from the posterior region of the oviduct. (For the entry of the pelvic vein see under this vessel.) If the injection is good it is usually possible to trace Jacobson's vein to the anterior extremity of the kidney, but its size in this region varies very much. It may remain fairly large, and anastomose with the post-cardinal vein, but more usually it tapers to an almost indistinguishable thread.

B. The *Common Iliac Vein* (v.il.com.). The blood from the hind-limbs has, in all Amphibia, the choice of two courses. It may go through the pelvic and abdominal veins to the liver, or it may enter the renal-portal system and pass through the kidney to enter the post-caval vein. It is to provide for this latter course that common iliac veins exist. Each lies on the dorsal side of the pelvis just posterior to the ilium and to N. spinalis 17, and dorsal to the common iliac artery of the corresponding side, and forms what appears to be the direct continuation of the V. ischiadica, but is marked off from this vessel by the origin of the V. iliaca transversa and the entrance of V. pudenda (see Figs. 62 and 63). The common iliac vein joins Jacobson's vein a short distance from the posterior end of the kidney and usually a little to the ventral side of that organ.

The *veins of the hind-limb* must, of course, be regarded as commencing at the distal extremities of the digits. The blood from the toes collects into the *digital veins* which lie along the sides of each digit, and, near the bases of the metatarsals, enter a transverse vessel lying across the dorsal side of the foot—the *Arcus venosus dorsalis pedis*. In addition to the above-mentioned veins from the toes this arc receives several tributaries from the extensor muscles of the foot and tarsus. In turn it delivers its blood into three main vessels. Of these two are superficial and pass along the tibial and fibular sides of the leg, corresponding respectively to the NN. dorsalis pedis tibialis and fibularis, while the third and largest vein is a deep vessel and courses in the interosseal space between the bones of the leg in company with the NN. dors. pedis intermedius and interosseus. It lies superficial to the A. interossea and deep to the above-named nerves. Just proximal to the knee these three veins unite to form a single large vein, which passes along the posterior aspect of the thigh together with the sciatic nerve.

This is rather different from the condition found in the Frog, but bears a much closer resemblance to Osawa's account of *Cryptobranchus*. The difference may probably be accounted for by the specialized nature of the hind-limbs in the Anura.

A comparison with the fore-limb and with Osawa's description

of *Cryptobranchus* suggests that the two superficial vessels may be called *V. lateralis cruris* and *V. medialis cruris* on the tibial and fibular sides respectively, and the deep vessel the *V. interossea*.

The main factors of the V. lateralis cruris.

(a) A *plantar vein* from the skin of the sole of the foot as well as from the muscles of the same region.

(b) A *cutaneous factor* from the plexus covering the extensor surface of the leg. Through this plexus communication with the *V. medialis cruris* is established.

(c) A fairly large factor from the deeper muscles enters the *V. lat. cruris* at about the middle of the leg. This factor anastomoses with one from the *V. interossea*.

(d) Just proximal to the knee one or two cutaneous factors from the flexor side of the leg are received.

(e) At about the same level a small muscular factor from the insertion of the *M. pub. isch. tib.* and the tissues around the knee-capsule enters the vessel.

At the knee the vein turns somewhat dorsalwards and passes into the thigh, dorsal to the *M. pubo-tibialis*, to join the *V. circumflexa genu*, which is itself a factor of the *V. ischiadica*.

On the post-axial or fibular side of the limb the *V. medialis cruris* arises from the *Arcus venosus dorsalis pedis* and receives a large factor from the dorsal plexus of the leg, whereby communication with the *V. lat. cruris* is established. Just distal to the knee it may receive a factor which drains the extensor and flexor muscles and lies close to the external border of the fibula, or this factor may enter the *V. poplitea* separately. At about the same point it receives a cutaneous factor which probably represents the *V. cutanea lat. sup.* (Gaupp) of the Frog. The main vein then turns into the thigh proximal to the knee and immediately dorsal to the *MM. ischio-flexorius* and *flexor fibularis*, between which muscles and the *M. extensor ilio-tibialis* it joins the *V. poplitea*.

The *V. interossea* is the largest of the three crural veins, and, as already mentioned, passes along the interosseal space together with the corresponding artery and nerves. It arises from the middle part of the *Arc. ven. dors. ped.* by factors which cross the dorsal side of the tarsus, deep to the extensor muscles, and unite to form a single trunk at its proximal edge. During the course of the vein down the leg it receives several factors from the surrounding muscles. Within the bend of the knee a cutaneous factor from the flexor side of the leg is received, as well as the *V. medialis cruris*. The vein may now

be called *V. poplitea*, and is soon joined by the *V. circumflexa* genu to form the *V. ischiadica*.

The *V. circumflexa* genu is a short vessel joining the sciatic vein almost at right angles just proximal to the knee. As stated above it joins the *V. lat. cruris*, while it also receives twigs from the knee-capsule and a *longitudinal recurrent vessel*, which lies in the thigh between the MM. pubo-tibialis and pubo-ischio-femoralis internus, i.e. along the anterior border of the limb. This vessel drains the adjoining muscles and also receives large cutaneous factors from the skin covering that region (possibly to be regarded as the *VV. cutaneae femoris anteriores mediales*). It is usually traceable towards the body as a very fine vessel which finally enters the pelvic vein, or anastomoses with a small factor thereof. There is therefore a continuous but ill-defined venous channel passing along the whole length of the pre-axial margin of the hind-limb, corresponding with the *V. brachialis lateralis* of the fore-limb, which is doubtless the homologue of the *V. femoralis lateralis* (Osawa) of *Cryptobranchus*. The position of this channel and the fact that it is the only vein entering the pelvic loop from the hind-limb *anterior* to the ilio-femoral joint would suggest that it is to be regarded as the representative, in the Salamander, of the femoral vein, which otherwise is wanting. A second anastomosis with the *V. ischiadica* occurs at about the middle of the thigh by means of the *V. circ. fem. med.* (see below), and hence the vessel may be called *V. collateralis femoris* (*v.col.fem.*).

The *V. ischiadica* (*v.is.*). After its origin from the union of the popliteal vein with the *V. circ. genu*, as above described, the sciatic vein continues along the posterior aspect of the thigh and receives the following factors.

(a) Posteriorly, the *V. profunda femoris posterior* enters from the MM. ischio-flexorius and pubo-ischio-femoralis externus and from the overlying skin. The cutaneous factor is the *V. cut. fem. medialis* (Gaupp).

(b) Mesially a pair of *VV. circumflexae femoris mediales* are received, one passing dorsal and the other ventral to the femur. They are both muscular factors draining the thigh muscles. The ventral one anastomoses with the *V. collateralis femoris*.

At the level of the hip-joint, in what Appleton conveniently terms the 'posterior groin', the *V. ischiadica* unites with the *V. iliaca transversa* and *V. pudenda* to form the common iliac vein. The sciatic vein thus forms the main vein of the thigh in the Salamander and carries almost the whole of the blood from the limb towards the trunk, whereas in the Frog (and in man and mammals generally) this function is

assumed by the femoral vein. In *Cryptobranchus*, judging from Osawa's account, the *V. femoralis lateralis* (=femoral vein) and the *V. femoralis medialis* (=sciatic vein) are approximately equal in size and importance. Hence there seems to be a twofold departure from the *Cryptobranchid* type, one where the *post-axial* vein becomes the important vessel—e.g. *Salamandra*—and the other in which the *pre-axial* path carries most of the blood—e.g. the Frog and the Amniota in general.

The *V. pudenda* (v.pud.) enters the proximal end of the *V. ischiadica* at the point where it merges into the common iliac vein. It arises in the female from the lateral wall of the cloaca, and in the male from the lateral portion of the cloacal gland, and runs antero-dorsally between the *MM. ischio-caudalis* and *caudali-pubo-ischio-tibialis*, receiving factors from both these muscles. At the dorsal border of the former muscle it receives an anastomosis from the median cloacal vein, while just before its entry into the ischiadico-iliac junction it receives several small cutaneous factors from the skin at the root of the tail, and sometimes a rather large anastomosis from the caudal section of the lateral vein, which probably represents a portion of the inferior lateral cutaneous vein of *Selachian* fishes.¹

The *V. iliaca transversa* (Rusconi) (v.il.tr.). Leaving the junction of the sciatic and iliac veins from the point where the *V. pudenda* enters, and passing round the dorsal side of the hip-joint to the region of the groin immediately beneath the skin, is a large vein which has been called *V. iliaca transversa*. It corresponds with the similarly named vein in the Frog, but it is a very much larger and more important vessel in the Salamander than in that animal. At the anterior edge of the ilium it enters the pelvic vein—in fact the major portion of the blood flowing through the ventral section of the pelvic veins into the abdominal vein arrives there through the *V. iliaca transversa*, since, in almost all cases, it is decidedly larger than the dorsal portion of the pelvic vein (cf. below).

Factors of the V. iliaca transversa.

(i) The anastomosis above described as sometimes entering the pudendal vein may enter the *V. iliaca transversa* direct.

(ii) The *V. cutanea femoris posterior lateralis* (Gaupp) from the skin covering the dorso-lateral aspect of the proximal portion of the thigh.

(iii) A twig from the *M. extensor ilio-tibialis*.

(iv) A cutaneous factor from the lateral parietes immediately anterior to the limb. This factor not infrequently anastomoses with the

¹ Cf. Daniell and Stoker 1927, and Daniell's *Elasmobranch Fishes*, California 1928.

abdominal portion of the *V. lateralis*, or with one of its factors, and enters the *V. iliaca transversa* close to the point where this vessel joins the pelvic vein. When the fusion between the factors of the lateral vein and the *V. iliaca transversa* occurs, the condition closely resembles that found in some reptiles, e.g. *Sphenodon* (O'Donoghue, 1921) and *Heloderma* (Beddard, 1906).

C. The *Pelvic Veins* (v.pel.), as in the Frog, offer an alternative course to the blood coming from the hind-limbs, and enable it to avoid the kidney. They arise normally on either side from Jacobson's vein a little anterior to the common iliac vein, and pass around the anterior rim of the pelvic basin, internal to all the muscles, to the mid-ventral line, where they fuse to form the abdominal vein. It is convenient to distinguish two sections in each pelvic vein, viz. a dorsal section from Jacobson's vein to the point where the *V. iliaca transversa* is received, and a ventral section from that point to the abdominal vein. The dorsal section varies considerably both as to its exact point of origin from Jacobson's vein and in size. It is never very large, and seems sometimes to be absent entirely. The ventral section is very much larger since it receives the considerable addition of blood from the *V. iliaca transversa*. It also receives the *V. parietalis lateralis* (v.par.l.) (lateral abdominal, of some authors) from the lateral abdominal muscles, and the small vein from the anterior aspect of the thigh joining the *V. collateralis femoris* (v.col.fem.) which may represent the femoral vein. Small twigs from the origin of the *M. pubo-ischio-femoralis internus* and from the insertion of the *rectus abdominis* muscles are also factors of this section of the pelvic vein.

Vessels of the Brain (Pl. IX, figs. 51 and 52).

A. **Arteries.** As already described the internal carotid artery passes into the cranial cavity through the carotid canal and the basi-cranial fenestra. In the cranial cavity it is known as the *A. carotis cerebialis* (a.car.ce.) (Schölb) which almost at once divides into a *R. anterieus* and a *R. posterius*.

(1) *R. anterieus* (a.ce.a.) (Schölb) courses along the lateral border of the thalamencephalon to the level of the optic chiasma, where it divides into dorsal and ventral branches.

(a) The *ventral* branch, *R. cerebialis anterior ventralis* (Osawa), *Arteria lobi haemisphaerici inferior externa* (Schölb), or more simply the *ventral cerebral artery* (a.ce.v.), runs along the ventro-lateral edge of the cerebrum as far as the olfactory nerves. From it vessels arise which form a rich network in the primary vascular coat (see 'Mem-

branes of the Brain', p. 123, et seq.). These do not arise periodically along the whole length of the vessel, but almost exclusively from near its origin, and at its anterior end. They are drained by the dorso-median vein of the cerebrum.

(b) The *dorsal branch*, *R. cerebrealis anterior dorsalis* (Osawa) (Arteria lobi haemisphaerici superior interna, Schölb) passes dorso-mesially round the thalamencephalon to the paraphysial region (nodus chorioideus, Rex), giving on its way a branch to the posterior and mesial regions of the cerebral hemisphere.

(i) The *mesial cerebral artery* passes anteriorly along the mesial face of the hemisphere somewhat obliquely in a dorso-ventral direction. This vessel does not appear to have been previously described unless it corresponds with the 'posterior dorso-median vein of the fore-brain' of Rex, which otherwise has not been found.

At the nodus chorioideus the dorsal cerebral artery sends a few small branches to the plexus and then turns ventralwards and divides into two branches.

(ii) One branch supplies the lateral plexus of the first ventricle (pl.ch.ven.1). The artery enters the ventricle through the foramen of Monro, and within it forms a very beautiful coiled plexus. If this plexus is carefully flattened out it is found to be roughly triangular in shape, with the artery bordering the perpendicular and base, and the veins gathering towards the apex.

(iii) The other branch supplies the *inferior median plexus* (Burckhardt's plexus chorioideus inferior), a small, but rich plexus lying in the recessus praeopticus.

The *superior median plexus* appears to be supplied usually by a branch from the right dorsal cerebral artery. This branch comes off just as the main vessel turns ventralwards. The plexus is long, tapered to a point at its posterior end, and flattened laterally. It lines in the dorsal part of the cavity of the diencephalon.

It should be noted that the right and left dorsal cerebral arteries are not always equal in size. Either may develop at the expense of the other.

(II) *Ramus posterius* (Schölb) or *R. cerebrealis posterior* (Osawa). This branch passes directly mesialwards to a point on the ventro-lateral border of the midbrain, just at the posterior border of the infundibulum and anterior to the origin of the IIIrd nerve. Here it breaks up into four branches.

(a) *R. opticus*, which ramifies fan-wise over the side of the optic lobe.

(b) The *R. pituitarius* which passes round the infundibulum to its ventral surface and then turns posteriorly to supply the pituitary body.

(c) *R. mesencephali superior* (Gaupp, Frog). This branch passes round between the optic lobes and the cerebellum. It supplies the latter, and finally terminates within the chorioid plexus of the fourth ventricle.

(d) *R. communicans* continues the direction of the main stem mesially, and anastomoses with the corresponding branch from the other side. From the transverse vessel thus formed there arises, in the middle line, the basilar artery.

The *Arteria basilaris* (a.b.) (Gaupp, Frog) arises by two or three roots, which almost immediately fuse to form a median vessel coursing along the mid-ventral line of the medulla oblongata, and giving numerous fine branches to it on either side. The auditory artery is given off just anterior to nerve V.

The *Arteria auditiva* (Gaupp, Frog) passes into the auditory capsule along with nerve VIII.

The A. basilaris is continued right along the vertebral column, where it is called the A. spinalis ventralis (Gaupp, Frog). It is the artery of the spinal cord.

B. Veins. It is not possible to give a connected account of veins of the brain since they converge on more than one point. The following description therefore commences at the anterior end of the brain and works backwards.

The *sinus sagittalis* (s.sag.) (Rex) is a vein of variable size. It arises in the primary vascular coat anteriorly and passes backwards in the middle line to the nodus chorioideus (Rex)—a triangular venous plexus in the paraphysial region (nod.ch.). At about the middle of its length it is considerably strengthened by the addition of a *dorso-median cerebral* vein (Rex, translated), bringing the blood from the hemispheres. The vein arises by the fusion of numerous factors from the ventral and mesial surfaces of the hemispheres, and, passing up between them in the sagittal cleft through the subdural space, enters the sinus sagittalis. It is not always possible to trace the sinus anterior to the entry of this vein. In any case it is very small. Rex has described two dorso-median cerebral veins, but only one has been found. It is possible he may have confused the mesial cerebral artery with the venous system (see p. 245). The blood from the various plexuses within the ventricles of the brain (see under 'Arteries') is also returned to the nodus chorioideus by numerous small veins.

The blood is carried from the nodus chorioideus by a pair of veins, one of which runs from each lateral angle of the triangular nodus.

The *oblique cranial* veins (v.cr.ob.) (Venae craniales obliquae, Gaupp, Frog) pass obliquely from the nodus chorioideus between

the posterior end of the cerebrum and the corpus opticum, and discharge into the venous plexus covering the sinus endolymphaticus (plexus lateralis, Schölb). About midway they receive lateral tributaries on either side.

Each *lateral cerebral* vein collects from the dorsal and lateral regions of the fore-brain.

The dura mater covering the diencephalon is fairly free from veins, and no vessel of any size occurs in it. The primary vascular coat, on the other hand, possesses a comparatively rich network of veins. This network collects into two dorsal longitudinal vessels (v.long.di.) near the middle line, which apparently correspond with the single, median, *Vena longitudinalis diencephali* (Gaupp) of the Frog. From the anterior end of these veins one or two vessels pass out through the subdural space and discharge into the plexus covering the sinus endolymphaticus.

The blood from the cerebellum collects into a vessel which enters the plexus covering the fourth ventricle.

The *lateral plexus* (pl.l.), covering the sinus endolymphaticus (Schölb's name is retained for sake of convenience), is a coarse venous network forming a hollow pyramid with a triangular base on either side of the diencephalon, the base being directed inwards and the apex outwards. The blood gathers into a single large vessel at the apex of the pyramid and passes out of the cranial cavity, ventral to the R. oph. profundus V, and enters the Vena petrosa lateralis (q.v.). This is the *Vena cranialis pro-otica* (v.cr.pr-ot.) (Gaupp), and is the *main* venous exit from the cranial cavity. It corresponds with the Vena cerebialis anterior of van Gelderen.

The anterior part of the fourth ventricle is roofed over by a very rich plexus, more or less rhomboidal in shape, and communicating at its anterior corners with the lateral plexuses. There is usually a fairly pronounced vessel running transversely across the anterior edge of this plexus. Entering the plexus dorsally are two *longitudinal medullary* veins which pass anteriorly along the borders of the posterior part of the fourth ventricle. They evidently correspond with the Venae craniales post-occipitales (Gaupp) of the Frog, but they are not nearly so pronounced in the Salamander, and do not communicate, other than very indirectly, with the Vena spinalis superior.

Rex has described for Triton several basal veins entering this plexus from the ventral side of the medulla oblongata, but, while the veins from the ventral side of the medulla of Salamandra certainly do communicate quite freely with the plexus, no vessels of sufficient distinction to warrant a name have been found.

There is, however, a *Vena communicans* forming an anastomosis between the *Vena cranialis pro-otica* of either side. It passes between the roots of nerve V, dorsal to the pituitary body, and receives a pair of tributaries therefrom.

The *pituitary* veins (v.pit.), one on either side, arise from the posterior edge of the pituitary body.

At the posterior corners of the plexus covering the fourth ventricle the network collects into a single vessel which also receives one or two basal veins from the ventral side, and then passes out of the cranial cavity together with the combined nerves IX and X. This is the sinus jugularis of Rex, but to avoid confusion with the jugular vein it may be called *Vena cranialis post-otica* (v.cr.po-ot.). It enters the occipital vein (q.v.) and is equivalent to the *Vena cerebialis posterior* of van Gelderen. In Triton it forms the principal venous exit, the *Vena cranialis pro-otica* being quite small (Rex).

The region of the medulla behind this point and the anterior section of the spinal cord are surrounded by an irregular, wide-meshed, venous network which again collects into a vessel leaving the neural canal through a foramen in the first vertebra, the *Vena post-occipitalis* (v.po-oc.) (Gaupp, Frog).

Almost immediately behind this point a definite dorsal longitudinal vein may be traced right down the spinal cord. This is the *Vena spinalis superior* (Gaupp), and collects the blood from the *Arteria spinalis ventralis*. It is connected with the *Venae post-occipitales* by a fairly definite branch.

SUMMARY OF VESSELS OF THE BRAIN.

It will have been noticed that the main arteries are almost entirely confined to the ventral surface, while the larger venous vessels occur dorsally. Further, the arteries are more closely applied to the neural tissue than are the veins. The connexions between the arteries and the veins within the substance of the brain have been shown by Schölb to consist of simple loops, which may be spirally twisted but never branched.

The vascular plexuses fall under three distinct heads:

(i) Those to which the blood is carried by arteries and drained by veins. These are the internal plexuses, viz. the *lateral* plexuses of the first *ventricle*, and the *superior* and *inferior median* plexuses of the *diencephalon*.

(ii) Those to which the blood is carried by both arteries and veins, viz. the *nodus chorioideus* and the *plexus* covering the *fourth ventricle*.

(iii) Those receiving their blood from veins only—the *lateral* plexuses covering the *sinus endolymphaticus*.

Rex describes all the plexuses as venous, although it is quite easy to trace the arterial connexions. He does not seem to have differentiated clearly between arteries and veins.

The roof of the diencephalon is peculiar in that it is comparatively free from blood-vessels, but is bordered by four large plexuses. It forms a sort of 'island'.

The main venous exit is alongside the Vth nerve, *anterior to the auditory capsule*. Smaller veins can usually be found leaving the cranial cavity together with most of the other cranial nerves.

LYMPHATIC SYSTEM

1. Historical.

Panizza (1833) was the first thoroughly to investigate the lymphatics of the Salamander, and, while his account is somewhat incomplete, and in one or two instances not quite correct, it is nevertheless a classic piece of work. His use of mercury as a medium for injection has been very sharply criticized by some later workers, notably Rusconi and Meyer, on account of the weight of this medium, which tends to deform the larger spaces. While this criticism undoubtedly has some justification it resulted in Panizza's work being discredited to an extent by no means deserved. Some five years later Bazin (1838–9) published a résumé of Panizza's work in French, but his extract of the portion dealing with *Salamandra* is very brief.

The work of the investigators immediately following Panizza (Rusconi, Meyer, Calori) was almost entirely confined to the lymphatics of the viscera and the sub-vertebral trunks (DD. thoracici). It is in this region that the distortion caused by mercury would be most evident, and hence attention was concentrated upon it.

J. Müller (1833) was the first to discover lymph hearts in the Salamander, and he described four, an anterior pair just behind the scapula and a posterior pair immediately caudad of the ilium. Meyer (1845) confirms the existence of these hearts and describes and figures an additional pair posterior to the scapula, making a total of six pairs. In 1884 Weliky showed that a whole row of segmentally arranged contractile bladders exists, lying along the sulcus lateralis between the dorsal and ventral body-muscles. He also investigated the histology of the bladders, and found that they were provided with muscles characteristic of lymph hearts. He says 'Die Muskeln der Lymphherzen sind bei beiden untersuchten Thieren' (*Salamandra*

maculosa and *Siredon pisciformis*) 'quergestreift, meistens spindel-förmig, mit excentrischen grossen Kernen'. Finally Greil (1903) completed our knowledge of the contractile portion of the lymphatic system by describing the central lymph heart, within the truncus arteriosus, dorsal to the aortic arches.

An excellent detailed study of the caudal lymph hearts and of the caudal lymph vessels was made by Favaro in 1906, while in 1912 Hoyer and Udziela undertook an investigation of the lymphatics of the larva. Their work is very thorough, and is based on direct observation by dissection of injected larvae as well as from serial sections of both injected and uninjected specimens. The condition they describe for the larvae needs but little amendment to make it applicable to the adult, the chief points of difference being the considerable extension of the jugular sinuses and the comparative diminution of the dorsal and ventral longitudinal vessels.

2. Technique.

The present investigation was carried out on animals that had been killed with chloroform and injected immediately after death with a semi-gelatinous mass made up as follows:

An appropriate quantity of best white gelatine is allowed to soak in a good excess of water for about twelve hours (overnight). The excess water is then drained off and the gelatine melted in the water it has absorbed. The resulting mass is referred to below as 'stock gelatine'. The injection mass consists of—

- 60 gm. stock gelatine (melted)
- 6 gm. potassium iodide
- 60 cc. pure glycerine
- 240 cc. sat. soln. of prussian blue in water.

This mass is liquid slightly above room temperature, but 'sets' to about the consistency of the white of an egg. It flows freely, and the prussian blue does not precipitate in the cannula, and, what is more important where the larger sinuses are concerned, is freely mobile without the injected mass breaking up or rupturing the walls of the vessel. The 'setting' is a delayed action so that cold apparatus may conveniently be used. It may be hastened by immersing the animal, after injection, in formalin. Gravity pressure of about 150 cm. of water was used for the injection, and, the point of the fine glass cannula having been inserted under the skin of the palm of one hand, the skin of the other palm and the soles of the feet were pricked with a needle, and the extreme tip of the tail was cut off. When the injection mass dripped more or less freely from all these four points

(10–15 mins.) the operation was stopped and all the points of exit sealed (with pyroxylin) so as to prevent leakage, and the animal immersed in 5–10 per cent. formalin overnight to assist in ‘setting’ the jelly.

3. Description (Pls. XVIII and XIX).

For convenience of description the lymphatic system may be divided into the following sections:

- A. Subcutaneous network.
- B. Lymphatics of the limbs.
- C. „ „ „ pelvic region and tail.
- D. „ „ „ trunk and viscera.
- E. „ „ „ pectoral region.
- F. „ „ „ head.
- G. Lymph hearts and their relation to the blood-vessels.

A. *Subcutaneous network.*

In contrast to the Frog there are no extensive lymph-sacs immediately under the skin, but, with the exception of a few more or less well-defined areas, the subcutaneous lymphatics form a rich reticulum with irregular meshes. The mesio-ventral portion of the abdomen is very sparsely supplied with lymphatics, which are almost confined to two small longitudinal vessels running along the mesial edges of the *M. rectus abdominis superficialis*, and receiving lateral tributaries segmentally at each myoseptum. Posteriorly these vessels join the sub-pelvic plexus, and anteriorly they enter the pectoral network. They represent the *trunci lymphatici longitudinales parabdominales* (Grodziński in *Amblystoma*). Lymphatics are also nearly absent from the dorsum of the trunk and tail, but are rich along the sides of the body.

The *sub-pelvic plexus* is a rich, subcutaneous network with irregular meshes, extending forwards from the cloaca on the ventral side of the body, between the legs, as far as the anterior end of the ypsiloid cartilage. It covers the *pelvic sinuses* (see p. 253) and to some extent the inguinal sinuses also. It communicates with the former sinuses on their ventro-mesial aspects at about the level of the transverse axis of the limbs.

The *sub-pectoral plexus* similarly underlies the pectoral girdle, and extends from the sternum to the gular fold. It becomes richer and sinusoidal laterally in the region of the arms.

The *sub-maxillary plexus* covers the whole of the skin of the mouth-floor, and becomes sinusoidal in the region of the gular fold. In

appearance it closely resembles a sinus in *Lacerta*, figured by Hoyer (*Anat. Anz.*, Bd. 73) and named by him 'Sinus thyroideus', but in *Salamandra* the glands lie much deeper than the plexus and are not associated with it. It therefore seems preferable to avoid this name.

The *lateral plexuses* underlie the skin right along the sides of the trunk and the base of the tail. They lie mainly ventral to the sulci laterales, but extend dorsalwards over the scapula and ilium. They are particularly rich in the neighbourhood of the limbs.

B. *Lymphatics of the Limbs.*

These were first described by Panizza with considerable accuracy, and later Hoyer and Udziela gave a more detailed account of their course in the larva. There is no essential difference between the fore- and hind-limbs so that a general description may serve both.

The whole limb is covered by a subcutaneous network which may be imagined as arising along the sides of the digits. At the bases of the metacarpals (or metatarsals) between the digits there are small lymphatic sacs which lead by short vessels into a palmar (or plantar) sac covering the whole ventral surface of the hand (or foot). This sac lies between the skin and the fascia of the superficial flexor muscles, and is penetrated by a number of fibrous threads which attach the fascia to the skin, so that the sac is broken up into a reticulum with very small meshes. It is in free communication proximally with the network covering the rest of the limb. In the region of the elbow (or knee) this network tends to drain into a pair of vessels passing along the pre-axial and post-axial sides of the proximal part of the limb, which latter in turn drain into the sacs lying around the shoulder and hip respectively. Small lymphatics also accompany the blood-vessels within the deeper parts of the limbs and communicate freely with the vessels just described.

C. *Lymphatics of the Pelvic Region and Tail* (Fig. 69).

On the ventral side of the pelvis is the sub-pelvic network above described. The greater part of this may be lifted as a sheet disclosing a series of three pairs of deeper sinuses, which, nevertheless, still lie superficial to the muscles. They may be called, from their positions, cloacal sinuses, pelvic sinuses, and inguinal sinuses respectively.

The *cloacal sinus* (s.ly.cl.) differs somewhat in extent in the two sexes. In both it extends as a broad sheet across the ventral surface, on either side of the cloacal opening. In the female it also extends dorsalwards lateral to the walls of the cloaca itself, while in the male there is a lymphatic network ramifying among the tubules of the

cloacal gland. The cloacal sinus has two communications with the vesicular sinus surrounding the base of the bladder, namely, one mesial, close to the middle line, and one lateral, passing in company with the pudendal vessels and nerve, which may accordingly be termed the *pudendal trunk*. Anteriorly the cloacal sinus is continued as the pelvic sinuses.

The *pelvic sinuses* (s.ly.pel.) lie on either side of the middle line beneath the pelvis, and consist of a very coarse and irregular network with small meshes. They drain the sub-pelvic network, and, in part, the cloacal sinuses, and finally enter the inguinal sinuses at their antero-mesial angles. A small vessel may usually be traced leaving the anterior extremity of the pelvic sinuses and passing along the lateral edges of the ypsiloid cartilage to join the para-epigastric trunks. The sinuses of either side communicate with one another by several small vessels.

The *inguinal sinuses* (s.ly.ing.) (sinus inguinales, of the German authors) lie lateral to the sinuses just described within the 'groin', and are really the ventral portion of a continuous sinus surrounding the base of the limb, the dorsal portion being known as the iliac sinus. After joining with the pelvic sinus anteriorly each inguinal sinus sends a trunk around the anterior and dorsal aspects of the limb which accompanies the V. iliaca transversa. This trunk receives the pre-axial trunk from the leg, and communicates freely with the subcutaneous network covering the ilium as well as with the iliac sinus.

The *iliac sinus* (s.ly.il.) is a rather irregular sac lying at the posterior aspect of the leg immediately behind the ilium. It stands at the junction of several large sinuses which meet in that region, namely, the post-axial trunk from the hind-limb, the inguinal sinus, and the vesicular sinus from the bladder. It also communicates freely with the subcutaneous network overlying it, and by means of this network a fair proportion of the lymph from the iliac region enters the lateral lymph hearts of the tail and is discharged by them into the V. lateralis (see p. 232). The rest of the lymph passes through the *truncus iliacus* accompanying the iliac artery and vein, to enter the subvertebral trunk.

All sinuses so far described are superficial to the muscles and skeleton. Immediately dorsal to the pubo-ischium, between it and the bladder, lies the *vesicular sinus* (s.ly.ves.). It is hammock-shaped and covers the ventral side of the neck of the bladder, and, as already mentioned, it communicates ventrally with the cloacal sinus, laterally with the iliac sinuses, while dorsally near its posterior margin it enters the peri-anal sinus.

The *peri-anal sinus* (s.ly.pan.), as its name suggests, surrounds the posterior end of the rectum, and lies between this portion of the gut and a sheath of fibrous tissue. It communicates ventrally with the vesicular sinus, dorsally with the subvertebral sinus, and laterally with the renal sinuses.

Panizza saw a part of the cloacal vessels and described some of the connexions between the lymphatics of the anus, cloaca, and bladder. Hoyer and Udziela commenting on his account state that these connexions are very much smaller and less important in the larva.

The *caudal lymphatics* have been described in considerable detail by Favaro for *Salamandra atra*. In the adult the main lymphatic trunks of the tail are the subvertebral vessels which run in the haemal canal and form a ladder-like network around the caudal artery. (According to Favaro there is only a single subvertebral trunk in the tail of Triton.) They are continuous with the subvertebral sinus of the abdomen. In the larva there is also a pair of lymphatic vessels just beneath the skin mid-dorsally and mid-ventrally—the *TT. lymphatici longitudinales dorsales et ventrales*, but in the adult only the latter persist, and that only as a very fine vessel passing along the mid-ventral line in the groove between the lateral myomeres.

D. *Lymphatics of the Trunk and Viscera* (see also Pl. XVI).

These vessels have received considerable attention from the earlier workers and have been largely used to discredit Panizza's work by drawing attention to the distortion caused by his use of mercury.

The lymphatics of the trunk comprise four pairs of longitudinal vessels.

(i) The *Trunci lymphatici longitudinales parabdominales* (t.ly.l.pab.) (Grodziński, in *Amblystoma*) have already been mentioned. They pass along the mesial edges of the M. rect. abd. superficialis.

(ii) The *TT. lymph. long. parepigastrici* (t.ly.l.pe.) (Grodziński) form a network around the epigastric arteries and veins. They are in communication posteriorly with the iliac and inguinal sinuses and anteriorly with the subscapular sinuses.

(iii) The *TT. lymph. long. laterales* (t.ly.l.l.) (Hoyer and Udziela) lie immediately under the skin in the sulci laterales.

(iv) The *TT. lymph. long. subvertebrales* (Hoyer and Udziela) are the largest of all and lie immediately ventral to the vertebral column (Fig. 63; t.ly.l.sv.).

The *TT. lymph. long. laterales* extend right along either side of the body from a short distance behind the sacrum to the posterior border of the scapula. They lie in the sulci laterales. In the larva they form fairly straight and well-defined vessels, but in the adult they assume a more zigzag course and are only distinguishable as larger vessels among the general lateral network. They are associated with the lateral lymph hearts, and through them discharge their lymph into the lateral veins. They are in communication posteriorly with the iliac sinuses by means of the subcutaneous network, while anteriorly they enter the subscapular sinuses. The relations between these trunks and the lymph hearts is further discussed on p. 260.

The *TT. lymph. long. subvertebrales*. Panizza supposed that the subvertebral lymphatic stem consisted of but a single trunk. Rusconi assented to this and said that the dorsal aorta and the vessels arising therefrom were totally surrounded by a lymph space as a finger is by a glove, and that the arterial walls were attached to the walls of the lymphatic vessel by fibrous bands. Meyer was of the same opinion. The dorsal aorta was thus supposed to be freely suspended in a lymph sinus. These earlier authors had not seen the caudal section, which was discovered later by Favaro.

By studying the larva Hoyer and Udziela showed that the subvertebral space is really to be regarded as a double trunk lying on either side of the aorta, the two elements of which are in frequent communication with one another by means of bridging vessels which pass both dorsal and ventral to the aorta. In the section between the kidneys the latter become so extensive as to give the appearance described by Rusconi. At about the level of the posterior extremity of the stomach, i.e. at the level of the pylorus, there is a large lymph sac extending ventrally between the mesenteric laminae—the cisterna linfatica (Panizza), while one limb of it extends into the ligamentum gastro-lienale. Into this sac the lymph from the whole gut drains, being carried thither by a number of small lymphatic vessels which run on either side of the blood-vessels. The lymph capillaries within the gut-wall are definitely external to the blood-vessels and they are arranged in different patterns, each characteristic of some particular region of the gut. On the stomach they form a fairly coarse, irregular, brick-like meshwork; on the duodenum and intestine they are arranged in a number of more or less parallel rows connected by bridge pieces so as to give a ladder-like appearance, while on the rectum the pattern assumes that of a rich small-meshed network.

From the subvertebral stem there are extensive lateral communications with what may be described as the renal sinuses.

The *renal sinuses* (s.ly.ren.) are extensive sacs occupying the space between the mesenteric laminae suspending the oviducts in the female, or the Wolffian duct in the male. They are particularly extensive in the posterior region and are interrupted only by the blood-vessels or ureters, which also traverse the mesentery. There are also smaller extensions into the mesovarium. The walls of the oviduct are richly supplied with lymphatic capillaries forming a network.

The pair of subvertebral trunks emerge again from the cisterna lymphatica anteriorly, and, although they are still extensively connected by bridges, their double nature is more apparent. At the level of the subclavian arteries a pair of transverse trunks pass out, parallel with these vessels, to the subscapular sinuses. The subvertebral trunks themselves follow the curve of the systemic arches, and, after joining with the axillary and jugular sinuses, enter the central lymph heart (see p. 260). It is convenient to call this loop *truncus peri-pharyngeus* (Fig. 70; t.ly.p-ph.). The section of the subvertebral trunks just described, i.e. the region anterior to the cisterna lymphatica, is the 'ductus thoracicus' of Panizza, who erroneously supposed that there was a single trunk only which split into two at the systemic arches. He also believed that the ductus thoracicus discharged into the subclavian veins. Meyer thought that the anterior bifurcation was an artificial production due to Panizza's use of mercury, and that the ductus thoracicus actually ended blindly in the region of the heart. This view is, of course, equally wrong.

Entering the subvertebral trunks dorsally are a number of segmental vessels from the dorsal muscles. Hoyer and Udziela have shown that, in the larva, these vessels anastomose with the T. lymph. long. dorsalis and send branches to the lateral lymph hearts, while in the anterior or 'thoracic' region they also fuse with one another to form a longitudinal vessel running close beside the vertebral column on either side. They call this vessel the *truncus lymph. long. paravertebralis*. In the adult it is not possible to trace the connexions with the dorsal vessel, which itself tends to disappear and is distorted by the development of the cutaneous glands, but the connexion with the lymph hearts exists, and it is possible to find some traces of the paravertebral vessel, although it shows signs of degenerating.

E. *Lymphatics of the Pectoral Region* (Pl. XVIII, fig. 68).

These are very extensive and paired in the adult, but the actual arrangement does not differ markedly from that of the larva. The largest and most important sinus in the pectoral region is the *subscapular sinus* (plexus axillares, Panizza). In the adult this sinus

becomes divided into two more or less distinct sections, namely, a *pars dorsalis* lying between the nerves of the brachial plexus and the scapula and forming the subscapular sinus proper, and a *pars ventralis* which, although in frequent communication with the former sinus, is separated from it by the nerves of the brachial plexus and by the subclavian artery. Its anterior extremity lies *ventral* to the aortic arches and is separated by them from the peri-pharyngeal trunk.

The *sinus subscapularis, pars dorsalis* (s.ly.sc.") receives the T. lymph. long. lateralis, a portion of the T. lymph. long. parepigastrius, the post-axial trunk from the fore-limb and the transverse trunk from the subvertebral stem already mentioned. Its lymph flows into the *pars ventralis* by two main tracks, one, a direct path, just anterior to the third spinal nerve, and the other by a circumflex route, the *T. lymph. circumflexus scapulae* (t.ly.circ.sc.), around the lateral aspect of the scapula, between the bone and the MM. *dorsalis humeralis* and *dorsalis scapulae*. This trunk receives the pre-axial trunk from the limb just before joining the *pars ventralis*, and also sends a branch directly forwards to enter the jugular sinus.

The *pars ventralis* (s.ly.sc.') is a large sac-like structure closely surrounding the roots of the main veins. In addition to the connexions with the *pars dorsalis*, already mentioned, the *pars ventralis* receives the remainder of the T. lymph. long. parepigastrius, i.e. the portion entwining the anterior epigastric veins (t.ly.l.pe.) and also a *sinus anastomoticus* (s.ly.anas.) from the *pars ventralis* of the opposite side. This sinus passes round through the fold between the pericardium and the peritoneum, ventral to the oesophagus, and somewhat dorsal to the posterior end of the ventricle. Entering the *pars ventralis* anteriorly are the *sinus thyroideus* (s.ly.th.), an elongated sac lying lateral to the thyroid gland, and a communication with the subcutaneous sinuses covering the M. *interhyoideus* posterior. The latter connexion penetrates the muscle and passes a short distance laterally over the dorsal side thereof before entering the *pars ventralis*.

The *pars ventralis*, in turn, discharges into the truncus peripharyngeus by means of several vessels that pass in mesialwards between the aortic arches.

Panizza supposed that the contents of this sinus flowed into the subclavian vein, which is undoubtedly incorrect, although, in the larva, Hoyer and Udziela show several fine connexions between it and the ductus Cuvieri and the anterior cardinal. The appearance in the adult, however, renders it extremely doubtful whether these communications persist. There are a number of fine lymph capillaries adhering very firmly to the bases of the internal jugular and subclavian veins,

but they may be scraped off without leaving any apparent trace, and while there *may* be some entry of lymph at these points it is very unlikely in view of the free passage for this fluid into the veins by means of the central lymph heart in the immediate vicinity.

F. *Lymphatics of the Head* (see also Pl. XIX, fig. 70).

These may be conveniently distinguished as 'dorsal' or 'ventral' according to their position relative to the mouth.

The *dorsal lymphatics of the head* (Fig. 70) are almost entirely confined to a pair of Y-shaped sinuses beneath the eyes—the *peri-orbital sinuses* (s.ly.p-o.). They were first described by Tretjakoff (1930). Each sinus lies in the posterior half of the orbit, between the M. levator bulbi and the skull, so that the bulbus oculi rests between the limbs of the 'Y', while the stem passes across the palato-quadrates and enters the peri-pharyngeal trunk. A small vessel from the peri-orbital sinus passes through the antrum petrosus laterale and enters the jugular sinus.

As Tretjakoff points out, in *Urodeles* lymph has replaced blood as a 'cushion' for the eye, enabling it to turn freely, since in fish that function is performed by the peri-orbital *blood* sinus.

Lymph capillaries are rich on the roof of the mouth and pharynx, and they also ultimately join the truncus peri-pharyngeus.

The *ventral lymphatics of the head* (Fig. 68) are much more numerous and extensive than the dorsal sinuses. On removing the skin there may be seen, in addition to the subcutaneous network already described, a lymphatic sinus running around the lower jaw—the *mandibular sinus* (s.ly.man.). At the posterior margin of the M. intermandibularis this sinus unites with the submaxillary network to form a common stem that passes dorsalwards between the above-named muscle and the M. interhyoideus and enters the sinus mandibularis profundus.

The *sinus mandibularis profundus* (s.ly.m.pf.) is a short sinus situated mesial to the angle of the lower jaw.

If the submaxillary network be removed, and the MM. interhyoideus and intermandibularis cut along the linea alba and turned back, the deeper sinuses may be traced. They probably arise from the tongue as the central organ, although the whole floor of the mouth and pharynx is rich in lymph capillaries. The lymphatics of the tongue drain into a *sacculus copularis* (sac.cop.), an irregular sac lying on the dorsal side of the copula, and the lymph flows therefrom by several alternative routes. In injected specimens the sacculus copularis may be seen extending anteriorly from the copula as a small

bladder from which pass two pairs of small vessels. Each pair accompanies the hypoglossal nerve of one side and enters the sinus thyroideus of that side. Between the radials on either side of the copula further bladder-like extensions of the saccus occur, which are drained by a pair of sinuses lying dorsal to the cerato-hyals. From their position they may be named the *hyoidean sinuses* (s.ly.hy.). Each joins the sinus mandibularis profundus of its side and enters the jugular sinus. On the dorsal side of the branchial cartilages on either side, and filling the space between them with the exception of that occupied by the M. rectus cervicis, is the *branchial sinus* (s.ly.br.). This also arises from the saccus copularis, but flows into the T. peripharyngeus. Its course between the posterior end of the branchial cartilages and the peri-pharyngeal trunk is sinuous and follows the lingual vein.

The *jugular sinus* (s.ly.j.) lies directly behind the corner of the mouth. Into it drain (i) the combined SS. mandib. prof. and hyoideus, (ii) the direct continuation of the S. circum. scap., and (iii) numerous small vessels from the occipital region, the thymus gland, and the antrum petrosum laterale. It discharges directly into the peripharyngeal trunk.

It must be noted here that the large space into which the posterior cornu of the hyoid projects is labelled by Drüner 'Sinus lymphaticus'. It is, however, *not* a true lymph sinus. Of the several injections that have been made in the course of the present investigation, in *none* has the injection mass used entered this space, neither has it been possible to find any opening therefrom. It therefore seems to be a closed sac of connective tissue whose sole function is to allow the free extension of the hyobranchial cartilages.

Extending posteriorly from the copula in the middle line is a *median sinus* connecting the saccus copularis with the Truncus peri-pharyngeus. It also receives many tributaries from the floor of the mouth.

G. *Lymph hearts and their Relation to the Blood-vessels* (Pl. XVII).

As previously mentioned there is a series of contractile vesicles along each side of the body in the sulcus lateralis, which place the lymphatic system in communication with the V. lateralis. There are normally fifteen pairs of these hearts. Four pairs are post-sacral, i.e. caudal, and the remaining eleven pairs lie between the sacrum and the posterior border of the scapula. There is some variation in size—those lying in the caudal and sacral regions being the largest, while those in the middle of the trunk are the smallest. Each heart lies embedded in the muscles directly behind the myoseptum, at the lateral extremity

of a rib. It is usually necessary to dissect away some muscle-fibres in order to expose them fully. Particularly is this so in the trunk region, but behind the sacrum they lie more superficially.

Lymph is received by each heart from two sources—first, from the T. lymph. long. lateralis, i.e. from the lateral subcutaneous network, and secondly from the parietal branches of the subvertebral trunks. The openings both into and from the hearts are guarded by valves. Figs. 65, 66, and 67, taken from Hoyer and Udziela's paper, show these relations clearly. The chief points in which the adult differs from the larva are, first that the hearts are more deeply embedded in the muscles, second that the T. lymph. long. lateralis pursues a more zigzag course, and is not so clearly defined, and third that there tends to be formed between each heart and the V. lateralis a short efferent stem, so that the heart is further removed from the vein.

Zaćwilichowski (1917) has studied the development of these lateral hearts in *Molge vulgaris* (presumably *Triton taeniatus*), and found that they develop from the wall of the vein, and later become secondarily associated with the lymphatic system.

There remains yet the *central lymph heart* (ct.ly.h.) to be considered. Its location in the truncus arteriosus has already been described (p. 190). To observe it the bulbus cordis must be severed near the ventricle and turned over anteriorly—then, if the muscles on the dorsal side of the truncus arteriosus be carefully removed, the lymph heart is revealed. The lymph enters from the T. peripharyngeus between the carotid and systemic arches and is discharged, posterior to the pulmonary arch, into the proximal portion of the lingual vein (V. pharyngea). Regurgitation at both entry and exit is prevented by valves. Greil's figures are a little misleading in that he shows the afferent vessels pointing directly forwards. According to Hoyer and Udziela they form a more oblique angle even in the larva, while in the adult their direction is almost transverse. The shape of the central lymph heart is roughly pyramidal, the base being directed forwards, while the apex is continued posteriorly as a fine vessel draining lymph from the bulbus cordis. The central lymph heart really lies dorsal to the truncus arteriosus, but, during development, it becomes enclosed by a strap-like band of cardiac muscle from the bulbus cordis that grows completely round between the right and left carotid arches and forms a continuous strip connecting the dorsal and ventral sides of the truncus arteriosus.

It is uncertain whether there is an intrinsic rhythm in the heart itself or whether the contraction is brought about entirely by the extrinsic muscles of its neighbourhood.

BIBLIOGRAPHY OF SECTION VI

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VII

THE ALIMENTARY TRACT AND ITS APPENDAGES, TOGETHER WITH THE SPLEEN AND THE MESENTERIES

THE ALIMENTARY TRACT (Pl. XXII)

1. General.

THE alimentary tract and the associated structures of the Salamander show a general similarity to those of the Frog, but there are several noteworthy differences. Of these the following may be mentioned: (i) the presence of teeth on *both* jaws, and the great backward extension of the pre-vomerine teeth; (ii) the relatively immobile tongue; (iii) the absence of Eustachian tubes opening into the pharynx; (iv) the fairly simple undivided liver; (v) the size and shape of the spleen.

2. The Mouth Cavity.

Owing to the fact that the outer skin is reflexed some distance dorsalswards at the angles of the mouth over the coronoid process of the lower jaw, there is a difference between the actual gape and the apparent gape. Thus the former extends to about the level of the posterior boundary of the eye, but the latter is continued a short distance behind this. There is only a slight suspicion of free 'lips', but the outer skin covering the jaws is glandular and contains the so-called *labial glands*.

The *teeth* are *pleurodont* and are directed inwards. They do not terminate in a single point but are bifid at the tips and sometimes tricuspid. There are slight differences in shape between the teeth in the various regions of the mouth, but for practical purposes the dentition may be termed *homodont*. The teeth are small and occur on both jaws as well as on the pre-vomers. The dentigerous processes of the latter extend far caudalswards to the back of the mouth, while their S-like shape is characteristic of true Salamanders, and, coupled with the short thick tongue, are definitive of the genus.

A detailed study of the teeth of Amphibia was undertaken by Hertwig (1874). He distinguishes two sections of each tooth—the *crown* which is visible above the gum, and the *socket* embedded in the

gum. The junction between these two portions is clearly marked. Three tissues combine to form each tooth, namely, dentine, enamel, and cement. These features may all be clearly seen by pulling out a tooth—which is quite easy—and staining it in a solution of alizarin in absolute alcohol and mounting it in balsam on a slide.

The mandibular and maxillary teeth serve merely to retain the food in the mouth, but the pre-vomerine teeth on the palate assist the tongue to work the food back to the pharynx so that it may be swallowed.

The *tongue* of the Salamander is a much less highly developed organ than that of the Frog, and consists simply of an oval pad firmly affixed to the floor of the mouth and with it to the copula of the hyobranchial apparatus. It is free laterally and to some extent posteriorly also, but nothing like to the same extent as the Frog's tongue. As Kallius (1901) has shown, the adult structure consists of a *secondary tongue* superimposed on a larval *primary tongue*. The *secondary tongue* forms practically the whole organ in the adult, and its epithelium, which is highly glandular, is thrown into deep folds arranged in a somewhat radial manner, so that the superficial area of the mucous epithelium is enormous. The *primary tongue* is just visible under the posterior edge of the secondary tongue. It is non-glandular. There is only a slight tendency for the secondary tongue to be bifid posteriorly. The ontogeny of the tongue as described by Kallius (1901) shows that the tongue of Salamandra exhibits a close recapitulation of the changes which Gegenbaur (1894) suggested had taken place during the evolution of this organ in the vertebrate series.

The mechanism whereby the tongue is extruded from the mouth in the act of seizing food is described on p. 61.

The epithelium of the mouth and pharynx is glandular and highly vascular, and is of considerable importance in respiration (see also p. 274, et seq.). In addition to this general glandular tissue there are two specialized sets of glands opening on to the roof of the mouth. These have been described in detail quite recently by Seifert (1932). The first and most important has long been known. It is the *glandula intermaxillaris* (or *internasalis*), and is situated between the nasal capsules. It discharges by two or three openings into a small median depression lying on the roof of the mouth immediately beneath the gland, and anterior to the pre-vomerine teeth. The other set of specialized glands are the 'Gaumendrüse' (Seifert) or *glandula palatina*, which open into a series of grooves on the bases of the

prevomerine teeth. These grooves and the median pit are easily discernible with a lens, but the actual openings of the glands must be sought in transverse sections under a microscope.

Kingsbury (1912) in *Salamandra atra* and various other Amphibia finds, in as many as twelve regions of the mouth and pharynx, aggregations of cells of a lymphoid character which he regards as analogous to the tonsils of Amniota. A detailed discussion of this question lies outside the scope of the present work, but the position of the following four patches, which Kingsbury finds to be definite and constant, may be mentioned.

(i) The *choanal* in the roof of the mouth immediately posterior to the internal narial opening.

(ii) The *lateral*, situated laterally in the pharynx in the general region of the articulation of the jaw.

(iii) The *sublingual* lying lateral to the tongue over the expanded cerato-hyal.

(iv) The *preglottideal* on the floor of the mouth just in front of the glottis.

It must be pointed out that Kingsbury's results are of a general nature and have not been checked specifically for *Salamandra maculosa*.

As in Amphibia generally the eyeballs are not separated from the palate by any skeletal element, and their form is therefore plainly visible as a pair of convex bulges on the roof of the mouth. Just in front of these may be seen a pair of relatively large oval openings, the *choanae* or *internal nares*.

3. The Pharynx and Oesophagus.

The *pharynx* leads directly from the mouth as a wide tube. It is richly vascular and unmarked by any Eustachian tubes and passes imperceptibly into a wide *oesophagus* (oes.) which in turn leads, also without any sharp line of demarcation, into the *stomach*. The external walls of both oesophagus and stomach, and in fact of the whole gut also, are smooth, but the internal walls are variously corrugated, each section of the gut having its own particular pattern. Thus the distinction between the oesophagus and stomach is clearer internally than externally, the lining of the former being thrown into deep longitudinal folds, while the folds of the stomach are marked by a relatively shallow, wide-meshed, irregular network, of which the longitudinal members are the more prominent. The mucous epithelium is velvety, and when scraped off the blood capillaries are found to be flat and not raised into loops.

Jacobshagen (1914) has made a comparative study of the relief pattern of the gut lining in Amphibia. He denies the presence of a pyloric valve in *Salamandra*—a conclusion which may be justly criticized.

4. The Stomach.

The *stomach* (stom.) is conical and lies almost longitudinally along the left side of the body. It narrows considerably at its posterior end, and there is always a well-defined constriction between this end of the stomach and the duodenum. The constriction is specially noticeable when the gut is full, and a slight thickening of the wall is discernible in longitudinal section, so that it seems impossible to avoid the conclusion that this constriction is indeed the *pylorus* (py.), although it must be admitted that it is less perfectly formed than in many animals, and it is doubtful whether the lumen is ever completely closed.

5. The Duodenum.

The *duodenum* (duo.) is short and is sharply reflexed along the mesial aspect of the stomach, but follows a more transverse direction relative to the body than does that organ. It is indistinguishable from the rest of the intestine except that it receives the pancreatic and bile ducts.

The *dorsal pancreatic duct* (d.p.d.), or rather the duct of the dorsal pancreas, enters the proximal end of the duodenum some 2 mm. or so from the pylorus. The *ventral pancreatic ducts* (d.p.v.), which belong to the two ventral pancreata, discharge into the common bile-duct which, in turn, enters the distal end of the duodenum, some 4–5 mm. from the dorsal pancreatic duct (see also p. 267).

6. The Intestine.

The *intestine* (int.) is a coiled tube of a regular diameter, approximately equal to, or slightly smaller than, that of the duodenum. Its length is about one-half that of the whole gut, measured from the pharynx to the cloaca. The pattern of the internal relief of the duodenum and intestine, considered as a whole, consists of a series of sinuous longitudinal ridges. The ridges are thick proximally—that is, at the duodenal end—but tend to become thinner and straighter towards the hinder end of the gut, until they are almost knife-like. If the mucous epithelium is scraped or brushed off it is seen that the underlying vascular network is also raised into ridges, and that

the capillary loops follow the same wavy outline. The network is much richer at the anterior end of the gut.

7. The Rectum.

The *rectum* (rect.), like that of the Frog, is an expanded flask-shaped structure arising quite suddenly from the posterior end of the intestine. It is much thinner walled than the rest of the gut. Crofts (1925) has described 'a small lateral "cul-de-sac" lying to the left side' of the rectum and containing lymphoid tissue, which she considers to be the homologue of the rectal gland of Elasmobranchs. It is supplied by the haemorrhoidal artery. It is often difficult to determine the exact location of this gland by direct observation, but is more easily seen when the rectum is full than when it is empty, as then it shows up against the dark faecal matter. The internal surface of the rectum is also traversed by longitudinal ridges, set fairly close together and thicker than in the intestine, but not so wide as in the stomach. It differs from the latter also in that the vascular network extends into the ridges. The rectum and urino-genital organs discharge their contents into a common cloacal chamber, but since the cloaca has a closer functional association with the latter organs it is described together with them (see p. 286).

THE GLANDS ASSOCIATED WITH THE ALIMENTARY TRACT

The *glands* associated with the gut, in addition to those already mentioned, are the *liver*, the *pancreas*, and the *spleen*. The association of the last-named with the stomach is topographical only, since it has neither functional nor developmental connexion with the gut.

1. The Liver.

The *liver* (liv.) is large, and only very slightly lobed. It lies ventral and to the right of the stomach, and, in the fresh condition, is dark red in colour. The *left side* of the gland is prolonged posteriorly into a thin leaf-like lobe. The backward extension of the *right side* is not so well defined nor so thin, but from this side of the liver there is a pronounced *dorsal* extension which encircles the post-caval vein, and which may hence be termed the *post-caval lobe*. It extends dorsally right to the point where the post-caval separates from the post-cardinal veins. The liver is completely suspended by mesenteries

(q.v.), and has a slight median cleft anteriorly where the ventral, or sub-hepatic, mesentery joins the lig. hepato-entericum.

There is a relatively large *gall-bladder* (gl.b.) lying just dorsal to the right lobe of the liver. In order to distinguish the details of the bile-ducts it is necessary to dissect away some portion of the liver tissue since they are completely embedded therein, with the exception of the common bile-duct itself which is embedded in the ventral pancreas.

Three main bile-ducts emerge from the liver (see Fig. 76). On the extreme right—left as viewed—is the *hepato-cystic duct* (d. h-c.) which bears the gall-bladder as a lateral expansion of its walls, and afterwards becomes the *cystic duct* (d.cy.), which is joined almost immediately by the *first hepatic duct* (d.h.'). The latter is separated from the former by the ventral hepatic artery. The *second hepatic duct* (d.h.") enters farther down, within the pancreas, so as to produce a very short *common bile-duct* (d.c.) into which the ducts of the ventral pancreas also discharge.

2. The Pancreas.

The *pancreas* (pan.) is roughly triangular in shape, and lies rather to the dorsal side of the duodenum, between it and the stomach. As Göppert (1891) and Choronshtsky (1900) have shown, the adult pancreas is a composite gland, representing three outgrowths from the embryonic gut, namely, two ventral and one dorsal. As already stated, the two ventral pancreata discharge their secretion into the common bile-duct, while the dorsal pancreas discharges by a separate duct directly into the duodenum. The pancreatic ducts are by no means easy to see by direct observation, but may be readily demonstrated by cutting a series of microtome sections of the duodenum. The three lobes of the embryonic pancreas become indistinguishably fused in the adult into a single mass.

THE SPLEEN

The *spleen* (sp.) is not strictly an appendage of the gut, but, since it is suspended from the left dorso-lateral wall of the stomach by the lig. gastro-lienale, and in part shares its blood-supply, it may conveniently be considered here. It is a comparatively thin, elongated ovoid body, some 10–15 mm. long by 4–4½ mm. broad. It is deep red in colour in the fresh condition. Choronshtsky holds that it is purely mesodermal in origin, while functionally it is of course a blood gland.

THE MESENTERIES

The mesenteries of the Salamander exhibit many interesting features. They have been investigated by Klaatsch (1893), Mathes (1896), and Brachet (1896). These authors are at some variance—in fact each seeks to correct his immediate predecessor, but the causes of their dissension lie in the mode of origin of the mesenteries rather than in their final relationships, so that it is unnecessary to enter into the long and rather involved discussion here. The following description therefore applies simply to the relations as they may be observed by the dissection of the adult.

1. The Dorsal Mesentery and its Derivatives (see also Pls. XX, XXI, and XXIII).

The *dorsal mesentery* (l.d.) attaches the gut to the dorsal body-wall. It is not quite a continuous sheet of membrane but is interrupted at the pyloric end of the stomach by a large circular hole, the posterior rim of which is bounded by the pancreas. Anteriorly the mesentery extends as far as the base of the lungs, i.e. approximately to the level of the anterior end of the ventricle of the heart.

The *gonads* are suspended by a pair of lateral diverticula from the dorsal mesentery which form the *mesovaria* (l.ms.) in the female and the *mesorchia* (l.mch.) in the male.

The *kidneys* are not suspended by a definite mesentery but lie fairly close to the body-wall; there is, however, a mesentery attaching the oviduct in the female, and the Wolffian duct in the male, to the outer edges of the kidneys.

The *spleen* is suspended from the left side of the stomach also by a reduplication of the dorsal mesentery. This fold is continued from both ends of the spleen as a 'tuck' in the mesentery. The anterior prolongation reaches to the stomach-wall and is the *plica gastro-lienalis* (Klaatsch), while the posterior extension is much longer and reaches to the rectum, and is the *plica recto-lienalis* (Klaatsch). It is important to notice that this latter fold does *not* follow the convolutions of the intestine, but stretches straight across the comparatively short distance between the posterior end of the spleen and the anterior end of the rectum, so that the whole of the convoluted part of the mesentery lies ventral to it.

2. The Ligamentum Hepato-entericum (l.h-e.).

Between the ventral side of the stomach and the dorsal surface of the liver there is a mesentery which carries the factors of the anterior

gastric vein and the branches of the dorsal hepatic artery. It is the lig. hepato-entericum. Its posterior margin ends freely at about the level of the bile-duct, while anteriorly it becomes attached to the post-caval vein, the pericardium, and the posterior wall of the trachea, where it ends.

3. The Ventral Mesentery.

The *Ventral Mesentery*, or lig. suspensorium hepatis (Rabl), as its name implies attaches the liver to the ventral body-wall. It continues posteriorly along the abdominal vein as far as the pelvic girdle, while anteriorly it ends at the pericardium.

4. The Ligamentum Hepato-cavo-pulmonale.

The *lungs* are not symmetrically related to the mesenteries. On the *left* the lung is supported only from the *dorsal* side by a reduplication of the mesentery supporting the stomach—the pleural ligament (l.pl.)—the posterior third of the lung (in the collapsed condition) being entirely free. The *right* lung on the other hand, in addition to being so supported, is attached to the liver by the *lig. hepato-cavo-pulmonale* (l.h.c.p.). This mesentery attaches the ventral surface of the lung to the lateral edge of the liver, and, as already stated, occurs on the right side only.

There yet remain to be mentioned a pair of mesenteric folds of considerable interest and importance. They are the *lig. coronaria hepatis* (l.c.h.) (Rabl) and extend from the abdominal openings of Müller's ducts—the ostia tubae—to the liver. The free edge of each fold forms the ventral lip of the funnel leading into the ostium, the dorsal lip of the funnel being formed by the *lig. tubae* (l.t.) (Rabl), which is a smaller fold joining the larger towards the liver. A similar ligament is also present in the male, although of course it is much smaller, and Rabl (1904), who has studied the development of this structure, states that, in the male, the normally single ligament may represent either the lig. tubae or lig. coronarium hepatis, the other having atrophied. The same author suggests that the lig. coronarium hepatis is homologous with the pleuro-peritoneal membrane of the mammalian embryo, which had been previously regarded as the anlage of the diaphragm (*vide infra*).

The *peritoneum* is a thin, loose membrane lining the abdominal cavity. It is only very loosely attached to the body-wall so that it is easily stripped therefrom. It is pigmented, but not heavily, the chromatophores being arachnoid.

5. The Diaphragm.

Although there is no thorax in Urodela and the lungs retain their primitive position in the abdomen, nevertheless the coelomic cavity is bounded anteriorly by precisely the same structures as it is in the Mammalia. The comparison between the Amphibia and Mammalia, and also with Birds and Reptiles, has been discussed in detail by Keith (1905), who regards the pleural coelom of Mammals as having been cut off from the abdominal cavity by the evagination of the lungs through the diaphragm, the points at which this occurred being marked by the pleuro-peritoneal openings of the embryo. Keith agrees with Rabl in regarding the pleuro-peritoneal membrane as 'merely a crescentic fold of peritoneum forming part of the genital mesentery'.

The three structures entering into the composition of the diaphragm in Salamandra are: (i) ventrally, a portion of the superficial stratum of the M. rectus abdominis which is closely attached to the ventral wall of the pericardium, while a few fibres are actually inserted into it; (ii) a central portion formed by the *septum transversum*, i.e. by the membrane dividing the pericardial coelom from the main body cavity; and (iii) a dorsal part formed by those fibres of the transversalis muscle-sheet which are inserted into the dorsal pericardial wall and around the tracheal chamber (cf. Fig. 77; m.t.).

Regarding the function of the diaphragm, Keith declares that it is *primarily* concerned with assisting the venous circulation of the abdominal cavity and filling the heart with blood by compressing the viscera, and that its respiratory functions are *secondary*. The latter function is *expiratory* in character in Salamandra, but becomes *inspiratory* in Mammalia, where the lungs are anterior to the diaphragm.

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VIII

THE RESPIRATORY SYSTEM, INCLUDING THE LARYNX

THE RESPIRATORY SYSTEM (Pl. XXIII, fig. 77)

UNDER this head it is proposed to consider those structures usually regarded as directly associated with the physiological process of respiration, namely the glottis, the laryngo-tracheal chamber, the bronchi and the lungs, and finally, to review the physiological aspect and to discuss the probable means by which re-oxygenation of the blood is brought about in the adult Salamander.

As is well known, the Caducibranchiate Urodeles employ the 'buccal-force-pump' method of breathing similar to that of the familiar Frog. This involves the presence of mechanisms for closing the nares, and for raising and depressing the floor of the mouth, but, as such structures are only secondarily subservient to respiration, they are described elsewhere in their appropriate places (see pp. 55 and 303).

1. The Glottis.

The *glottis* (gts.) is a small slit-like aperture lying longitudinally on the floor of the pharynx. It is raised only very slightly above the level of the surrounding tissues, and leads directly into the laryngo-tracheal chamber.

2. The Laryngo-tracheal chamber.

The *laryngo-tracheal chamber* (tr.ch.) is a more or less triangular cavity. The glottis opens into the apex, antero-dorsally, while the posterior basal angles merge into the bronchi. The whole structure lies immediately dorsal to the truncus arteriosus, which thus forms a useful landmark for dissection purposes. The sides of the chamber are supported by a series of semicircular cartilages, the whole series forming the *cartilago lateralis* (Edgeworth),¹ while the anterior pair are distinguished as the *pars laryngea s. arytenoid* (Edgeworth), and the remainder as the *pars trachealis* (Edgeworth). The *arytenoid cartilages* (c.ary.) bound the sides of the glottis and are approximated

¹ The synonyms of other authors are sufficiently obvious to render citation unnecessary.

by the *M. constrictor laryngis* and pulled apart by the *M. dilatator laryngis*. These muscles are described on p. 64.

3. The Bronchi.

The *bronchi* are short, wide tubes leading directly from the posterior angles of the laryngo-tracheal chamber to the lungs. Their epithelium is ciliated (Suchard).

4. The Lungs.

A very good account of the *lungs* has been given by Suchard (1903), who deals with their minute, as well as their gross structure. They consist of a pair of small, heavily pigmented, conical sacs, pointed posteriorly, and presenting a sacculated appearance externally. Their cavities are not simple but are interrupted by trabeculae. According to Suchard, two main longitudinal compartments may be recognized, containing respectively the artery and the vein, together with subsidiary longitudinal compartments formed around the arterioles and venules, while the transverse septa are merely folds in the pulmonary membrane. The same author states that smooth muscle elements are present, but apart from these the lungs would be satisfactorily compressed by the muscles of the abdomen. The lungs are not suspended freely in the pleuro-peritoneal cavity as are those of the Frog, but are firmly anchored dorsally to the body-wall by the pleural mesenteries, and ventrally to the liver by the lig. hepato-cavo-pulmonale (see also p. 269).

Homologies of the Urodele Larynx.

A great deal of work has been published on this question and various authors have advanced different theories in an attempt to demonstrate that the arytenoid cartilages and the laryngeal muscles represent the remains of a transformed visceral arch.

The discussion began in 1892, when Wilder and Gegenbaur independently advanced similar theories. Wilder suggested that the *pars laryngea cartilaginis lateralis* really represented the cartilage of the fifth branchial arch of Selachians, and that the *M. dilatator laryngis* was homologous with the dorsal segment of the muscles of that arch. He also thought that the ring of muscle surrounding the larynx—*M. constrictor laryngis*—was a continuation of the circular muscle of the alimentary canal, and that the *pars trachealis cartilaginis lateralis* arose later than, and independently of, the arytenoids from

the surrounding tissue. In other words he claimed that the *cartilago lateralis* had a dual origin.

Gegenbaur's theory was very similar except that he thought that the whole *cart. lateralis* was derived from the fifth branchial arch, and that the *M. transversus ventralis* was homologous with the *constrictores arcuum* of that arch. Göppert (1894) accepted Gegenbaur's theory and said that the *M. dilatator laryngis* represented *M. levator arcuum V*, and was therefore the homologue of the *levatores* of the branchial arches. He opposed Wilder's theory as to the derivation of *M. constrictor laryngis* on the ground that it is a striped muscle, while the circular muscle of the alimentary canal is of course composed of smooth elements.

In 1896 Wilder returned to the subject. He renounced his former theories concerning the dual origin of the *cart. lateralis* and derivation of the ring of muscle round the larynx from the muscles of the gut, and accepted the views of Gegenbaur and Göppert. Göppert (1898) also abandoned his former theory that the *M. laryngeus ventralis* is derived from the transverse muscle of the fourth branchial arch and said that it was really a serial homologue of this and represented the *M. transversus ventralis V*.

In 1901 Drüner published his classic work on the visceral skeleton and its muscles in Salamandra and Triton in both larval and adult stages. He declared a general acceptance of the current theories but, on the ground of innervation, suggested that the laryngeal skeleton and its muscles were not derived from the fifth branchial segment but from the sixth or some more posterior arch.

Wiedersheim (1904) was the first to put forward the suggestion that perhaps the *cart. lateralis* of Amphibia had no connexion with the visceral arches after all, but was rather a supporting structure produced independently in response to muscular pressure. This suggestion was based on his study of the Ganoid and Dipnoan fishes (*Zool. Jahrb. Suppl.* vii, pp. 1-66).

Edgeworth (1920) turned Wiedersheim's suggestion into an established fact. After giving an anatomical description of the development of the laryngeal structures in various Amphibia, he reviews the work of previous investigators and then summarizes his own conclusions in the following words:

'The arytenoid s. pars laryngea cartilaginis lateralis of Amphibia is developed within the constrictor laryngis, or within this and the laryngei, and like them is differentiated from cells from the splanchnic layer of the coelomic epithelium. It does not therefore represent a fifth, or a more posterior branchial bar. Its development is probably, as Wiedersheim suggested, dependent on muscular

action. It is possibly related to the new development of the dilatator laryngis in Amphibia. The tracheal skeleton s. pars trachealis cartilaginis lateralis is a backward prolongation of the arytenoid and related to the development of the trachea.

It must be noticed that an excellent description of both the muscles and the skeleton of the larynx of *Salamandra* was given as early as 1839 by Henle, but he made no suggestions as to the homologies of the several parts.

Physiological Considerations.

It is well known that the common Frog is capable of respiring to a large extent through the skin as well as through the lungs. That Caducibranchiate Urodeles are also not entirely dependent on pulmonary respiration is obvious from the fact that many are devoid of lungs altogether, e.g. *Eurycea* (*Spelerpes*), *Salamandrina*, &c., while the lungs of other forms, e.g. *Triton*, are mere hollow sacs with smooth walls which present only a relatively small surface to the contained air, and are probably hydrostatic rather than respiratory in function. In support of this latter statement Lönnberg (1899) points out that all aquatic Urodeles devoid of lungs *crawl* rather than *swim*. Numerous experiments have been carried out, by Camerano and others, with the object of discovering to what extent the skin acts as a respiratory medium. These have been well summarized by Bethge (1898), and it is not proposed to discuss them here. They are none of them free from the objection that they do not ensure the absence of secondary effects being introduced which may affect the general health of the animals being treated. Bethge himself draws attention to the interesting fact that the cutaneous capillaries of *Salamandra*—where the lungs have an undoubted respiratory function—have only about one-half the diameter of those of *Eurycea* (*Spelerpes*), an animal entirely devoid of lungs, while in *Triton*—whose lungs are largely hydrostatic in function—the capillaries of the skin are about intermediate between the other two. It therefore seems probable that the skin has *some* influence in respiration but only to a slight extent in *Salamandra*.

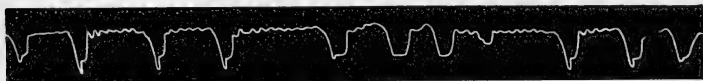
In 1906 Whipple made a careful study of the respiratory movements of pulmonate Urodeles, and, while she did not use *Salamandra* itself, her conclusions are quite applicable to that animal. She finds that there are two forms of respiratory movements in Urodeles possessing lungs. The first consists of a shallow oscillation of the floor of the mouth which takes place rapidly and continuously, and

involves only the air contained in the mouth and pharynx. This is known as *bucco-pharyngeal* respiration. The second is more complicated and involves the lungs, so that it is conveniently referred to as *pulmonary respiration*.

More recently Willem (1923 and 1924) has carried out experiments on the respiratory movements of the mouth-floor of a large number of Amphibia, both Urodele and Anuran, including Salamandra, and has taken tracings of these movements by means of a stirrup placed under the head and attached to a pointer. (Text-figs. 1, 2, and 3 are taken from his work.) Text-figure 1 is one



TEXT-FIG. 1. A tracing of the movements of the floor of the mouth, taken by means of a stirrup passing under the head, reading from right to left. The ordinates are magnified by 5 and the speed is 4 mm. per sec. The change in the level of the tracing is due to a movement of the head. (After Willem.)

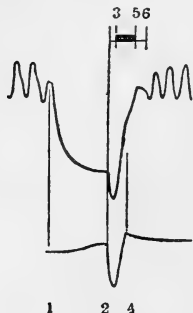


TEXT-FIG. 2. A tracing of the periodic variations in the amplitude of the pulmonary expirations. Read from right to left. (After Willem.)

such tracing in which the ordinates, representing the amplitude of the oscillations of the mouth-floor, are magnified by five, the ribbon at the same time passing under the needle at the rate of 4 mm. per second. The movements involved in pulmonary respiration are represented towards the right-hand side of the figure as a deep depression in the otherwise more or less regular succession of bucco-pharyngeal movements. Text-figure 2 shows that there is a rhythmic variation in the amplitude of the pulmonary respirations, while text-figure 3 is an enlarged detail of one series of movements involved in filling and emptying the lungs. According to Willem the bucco-pharyngeal respirations occur at the rate of 120 per minute and have an amplitude of nearly 2 mm. The interval between successive pulmonary respirations depends on circumstances. When the animal is in a state of repose it is about fifteen minutes, but if the animal is

excited, or moving, or is fatigued through being handled, the interval becomes much shorter.

The complicated movements carried out to effect the filling and emptying of the lungs are as follows. The depression of the mouth-floor is exaggerated and prolonged. The external nares are open during the first part of this act and the air is drawn into the mouth. This process is known as *aspiration*. Just as the mouth-floor is approaching its lowest point the nares are closed, or nearly so, so that the residue of air is drawn from the lungs and mixed with the pure air already in the mouth. This process is called *expiration*. The mouth-floor then rises and, the nares remaining closed, the mixed air is forced into the lungs. This constitutes the act of *inspiration*. The nares then open again and there follows a longer or shorter period of bucco-pharyngeal respiration before this more complicated process of *pulmonary respiration* is repeated.



TEXT-FIG. 3. Diagram of the respiratory movements of the Salamander, comprising the closure of the nares (upper line), the movements of the mouth-floor (upper tracing), and the pulmonary pressure (lower tracing). (After Willem.)

1. Commencement of aspiration.
2. Opening of the glottis and the commencement of the closure of the nares.
3. The nares completely closed.
4. Closure of the glottis.
5. Commencement of the opening of the nares.
6. The nares completely open.

to the surface, actually pushing into the epithelial layer, between the cells.

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IX

THE URINO-GENITAL SYSTEM

General and Historical.

THIS is perhaps the most widely and most accurately known system in the entire animal. The majority of the older authors made more or less accurate observations so far as the gross anatomy of the kidneys, gonads and their ducts is concerned (see Historical Introduction). Apart from such accounts the earliest author to study the system in any detail was Leydig (1853), who added many histological observations to his account. He observed and figured the *receptaculum seminis*, but failed to realize its function. He also recognized and correctly described the adrenal bodies, and he further figures and describes a curious pear-shaped epithelial bladder attached to the vestigial Müller's duct in a male specimen, which he thought was a vestige of an anterior part of the kidney (he of course did not realize the true significance of Müller's duct but thought it was connected with the ureters). Spengel (1876), the next worker of note, was unable to find anything which would correspond with the structure described by Leydig. Spengel's account of the urino-genital system of Amphibia is very detailed and accurate, and embraces all three classes (Gymnophiona, Urodela, and Anura) involving a number of genera in each class, and includes Salamandra. It is mainly owing to his labours that the anatomy of this system is so well known, and he deals not only with the macroscopic structures but also with histological details of the kidney tubules, &c. There has been no subsequent paper worthy of note dealing with the entire system, although a number of authors have treated particular sections in more detail. Their papers will be referred to later in the appropriate places. A possible exception may be made with regard to Fürbringer's paper (1878), which deals with the development of the organs concerned, while Gray's (1932) work on the development of the mesonephros in Triton throws much light on the general condition of this organ in Urodeles.

The urino-genital system of Salamandra generally, and of the male particularly, is very interesting, since it shows an even more primitive condition than is found in the Selachians in that the anterior part of the kidney is less specialized for a purely genital function, and retains clear evidence of its segmental nature.

The kidneys in both sexes are paired and symmetrical and are very much more elongated than they are in the Frog. Each is narrow and ribbon-like anteriorly and becomes wider and thicker posteriorly. The former portion, called the 'sexual kidney' on account of its association with the gonad in the male (*vide infra*), is a true mesonephros. The recent work of Gray referred to above shows that in Triton the 'sexual kidney' is sharply defined from the posterior portion in its developmental history. He calls the latter the 'definitive kidney' and says that in this portion the *primary* definitive units arise from a set of vesicles distinct from those of the sexual part, and that these primary units eventually serve as collecting ducts for the *secondary* definitive units which bud off from them. There is thus not only a differentiation of function but also of fundamental structure in the two portions of the kidney.

It is of course unsafe to assume that the developmental history of the Salamander's kidney is *identical* with that of Triton, but there is every reason to suppose that it is *similar*, particularly as far as the 'definitive kidney' is concerned. The 'sexual kidney' is quite different in macroscopic appearance, and hence developmental differences are more likely to be present in this region if anywhere. Ciliated nephrostomes are present, but show a degenerative tendency in the sexual kidney of the male (Spengel). The glomeruli are easily observed with the aid of a dissecting microscope, either directly in a freshly killed specimen or after injection with Prussian blue. The Malpighian bodies of the 'sexual kidney' are very regularly—but not segmentally—arranged in a linear row, while in the 'definitive kidney' the arrangement is necessarily more complex.

Adrenal bodies are present and appear as small orange patches on the ventral surface of the kidneys in both sexes. They are not, however, confined to the kidneys as they are in the Frog, but may be found anterior to them, as far as the subclavian artery, associated with the sympathetic ganglia.

In both sexes there is to be found lying in the dorsal mesentery, ventral to the aorta, about 7 mm. posterior to the subclavian artery, a pair of small pear-shaped bodies, looking, at first sight, rather like large sympathetic ganglia, although they vary considerably in size and appearance. They seem to represent the structure described and figured by Leydig (see p. 277), but he found it on the right side and in the male only, whereas that described here normally occurs on both sides and in both sexes. Leydig thought that the structure was connected with Müller's duct, which is certainly not the case. It is, however, richly vascular and is connected with the

dorsal aorta and the post-cardinal veins. A microscopic examination of a series of transverse sections reveals its epithelial nature, and, while a few nerve-cells may be present, it is definitely not a ganglion, and their presence must be regarded as incidental and consequent on its close proximity to a true ganglion of the sympathetic chain. While, as already stated, the appearance of these bodies varies considerably, they not infrequently consist of a hollow epithelial vesicle with a knot of cells towards one side—in other words, they are strongly reminiscent of an abortive Malpighian body. At other times they are more dense and do not exhibit this appearance. Although an investigation of their embryological history would be necessary in order completely to elucidate their identity, it is suggested that they are probably of nephric origin and may possibly represent the vestige of a pronephros.

Since there are definite sexual differences in the shape of the kidneys as well as in the arrangement of the ureters it is necessary to consider each sex separately.

THE FEMALE SYSTEM (Pl. XX)

1. The Kidneys and Ureters.

The two sections of the *kidney* as outlined above are distinguishable, although the 'sexual kidney' is such in name only since it has no connexion with the female gonad. It also merges more gradually into the definitive kidney, which in turn is somewhat smaller in the female than in the male. The *ureters* (utr.) or *Wolffian ducts* are very different in the two sexes. In the female the duct of the 'sexual kidney' is a very fine longitudinal canal lying close alongside its lateral edge. This duct is joined at intervals by about eight transverse tributaries from the tubules of the kidney. As it approaches the 'definitive kidney' the Wolffian duct diverges somewhat from its edge and passes backwards via the mesentery supporting the oviduct and, like this duct, becomes folded over to the ventral side of the kidney just before entering the cloaca. It receives tributaries from the kidney all the way along, and becomes correspondingly thicker. The fact that these tributaries enter the Wolffian duct approximately opposite the point where they leave the kidney is in strong contrast to the condition in the male. The duct opens into the cloaca at the apex of a small papilla just dorsal to the opening of Müller's duct (oviduct). It remains entirely separate from Müller's duct throughout its length, and does not discharge into it as some of the early workers supposed.

2. The Ovaries.

The *ovaries* (ov.) are paired and are either symmetrically placed or else the right ovary is slightly anterior to the left, but the asymmetry is not so marked as in the case of the male gonad. The actual appearance and size of the ovary naturally depends on the season at which the animal was killed, but, assuming it to be approaching ripeness, it will measure about 30 to 35 mm. long and will contain some 7 to 20 large eggs about 3 mm. in diameter surrounded by numerous smaller ones. The eggs are very heavily laden with yolk and have no black pigment but are deep yellow in colour. The ovaries are supported by the mesovaria from the mesial side of the kidney, and resemble those of the Frog in structure in so far as they are enclosed in an *ovisac* which must be ruptured to allow the ripe eggs to escape into the coelom. The internal openings of the oviducts into which the eggs make their way, probably assisted by ciliary action, are situated near the bases of the lungs as in the Frog. In many, if not in all, females some vestiges of *vasa efferentia* and of *Bidder's duct* (which are only functional in the male, see p. 286) may be found. In any case these structures are hardly visible to the naked eye and are best sought for along the mesial edge of the kidney where the mesovarium is attached.

3. The Fat-body.

The *fat-body* (ft.b.) is markedly different from that of the Frog, both in position and shape. In the female it is suspended from the mesial aspect of the mesovarium and is a narrow ribbon-like structure, golden-yellow in colour, containing numerous fat globules which give it a spangled appearance. The seasonal variation in size is quite inconsiderable, and according to Funke (1899), it can have but small influence as a somatic reserve. Apparently this function is mainly undertaken by the liver, which, in *Salamandra*, is characterized by a high fat content. Considerable fat reserves are also to be found in the cavities of the bones, around the spinal ganglia, and in the connective tissue between the muscles.

4. The Oviducts (Müller's Ducts).

The *oviducts* (*Müller's ducts*) (od.) are a pair of white convoluted tubes passing the whole length of the abdominal cavity. They are never pigmented in the female. They open into the coelom at the *ostia tubae* (ost.od.i.) situated just lateral to the bases of the lungs, and the ostia in turn expand into large funnels bounded by the

ligamenta tubarum (l.t.) and the ligamenta coronaria hepatis (l.c.h.)—see also p. 269. The oviducts open separately into the cloaca (ost.od.e.). Their lips protrude somewhat and are incised so as to give the openings a star-shaped appearance. The actual appearance of the oviduct within the abdomen will depend on whether the animal is pregnant or not, but in either case two regions are distinguishable, namely, an anterior convoluted portion which is dead opaque white with thick glandular walls, and a posterior 'uterine' portion in which the larvae develop. The latter part is thinner walled and is not convoluted, and it is this portion which alters very considerably in size and appearance during pregnancy. The figure (Fig. 72) was drawn from a female devoid of embryos and gives a good impression of the relations of the oviduct under such conditions. When the animal is pregnant, however, the 'uterine' portion (i.e. the portion posterior to the ‡ in the figure) elongates very considerably and becomes doubled on itself, protruding far forwards into the abdomen. In other words the junction between the glandular 'oviducal' portion and the 'uterine' portion remains fixed near the posterior end of the abdomen, so that the enlargement and elongation of the latter part must necessarily produce a duplicated loop as above described. The result is very striking in the early stages of the development of the eggs, when the whole structure has the appearance of a string of beads enclosed in a semi-transparent envelope. It will also be noticed that the arrangement of the veins is different in the two portions. The blood from the glandular part drains into the longitudinal oviducal vein (v.od.long.) which in turn discharges into the post-cardinal vein, while the 'uterine' portion drains by numerous tributaries (v.od.p.) directly into Jacobson's vein. Stüve (1889) incorrectly describes the vascularization of the oviduct since he thought that there was actual extravasation of blood from the capillaries, which he compared with the menstruation of Mammals. A year later Wiedersheim committed the same error with regard to *S. atra*, but Schwalbe (1897) and Noble (1927) have corrected these mistakes and have shown clearly that the blood is normally confined to the capillaries. Nevertheless the whole 'uterine' region is very vascular, the capillaries forming a rich network immediately beneath the epithelial lining.

Much has been written with regard to the development of the Müllerian ducts in Amphibia and only a very brief summary of this work can be given here. Fürbringer (1878) believed that they split off from the Wolffian ducts, while on the other hand Gregg Wilson (1896–8) found that the Müllerian ducts arose from the

peritoneal epithelium independently of the Wolffian ducts. Gemmill (1897) took a view midway between these two extremes and held that the anterior part of the oviduct arose as Wilson described from a peritoneal evagination, but that the posterior portion was formed by splitting off from the Wolffian duct. Finally Rabl (1903-4) affirms that the funnel is formed from the metamorphosed 'second' nephrostome of the pronephros, and that the part of the duct immediately posterior to this, forming the anterior part of the duct, is formed by a thickening of the coelomic epithelium which then grows backwards independently to form the posterior part of the duct. Hall (1904) confirms this mode of origin for *Amblystoma*, and hence it may be accepted as a final verdict on this vexed question.

5. The Receptaculum Seminis and the Cloaca.

The *cloaca* of the female is a simple chamber into which open the ureters, the oviducts, the rectum, and the urinary bladder. As mentioned above, the openings of the ureters are situated immediately dorsal to the oviducal openings, which, in turn, lie on either side of the rectum, while the opening of the bladder lies directly beneath them ventral to the anus. The external opening of the cloaca is a longitudinal slit which, in the female, lies flush with the surrounding tissues and is not possessed of tumid or swollen lips. The lateral and dorsal walls of the cloaca are thrown into deep furrows, while on the dorsal wall, just behind the oviducal openings, may be seen a pair of pigmented patches. These mark the position of the *receptaculum seminis* (rec.sem.) which is usually considered to be the homologue of the pelvic gland of the male (see p. 287).

The *receptaculum seminis* was noticed and described by Leydig (1853), but he did not observe the sperms within it, and did not realize its significance. This omission was supplied by von Siebold, who is usually credited with the discovery some five years later (1858). The organ consists of a number of small finger-like pockets protruding dorsally from the roof of the cloaca, which imbibe the sperms liberated from the spermatophore after it has been taken up into the cloacal chamber of the female (see also p. 5). The sperms are apparently able to, and normally do, live for a considerable time within the receptaculum.

6. The Urinary Bladder.

The *urinary bladder* (Fig. 63, bl.) is a large bilobed sac with very thin walls lying ventrally in the posterior abdomen between the rectum and the pelvic girdle. It extends anteriorly almost as far as

the posterior margin of the liver, closely adherent to the abdominal vein. Its walls, though thin, are well supplied with blood-vessels. There is no direct connexion between the bladder and the ureters, so that the urine can only gain access to it through the cloacal chamber (see also p. 287).

THE MALE SYSTEM (Pl. XXI)

1. The Kidneys and Ureters.

The chief differences to be observed between the kidney of the male and that of the female are the sharper distinction between the 'sexual kidney' and the 'definitive kidney', and the greater relative size of the latter. The 'sexual kidney' in this sex is directly associated with the gonad and serves to connect the vasa efferentia with the Wolffian duct, while the sperms actually pass through its tubules. Since Malpighian bodies are also present in the 'sexual kidney' it is presumably able to secrete urine, and hence its duct must be looked upon as a true urino-genital (Wolffian) duct. A much more striking difference between the sexes is noticeable in the *ureters* (utr.). In the first place although they are only small as they leave the kidney, they expand very rapidly and become much larger in the male and thicker walled (= appendices penis glandulosae, Funk), and secondly the urino-genital duct draining the 'sexual kidney' is not joined by the purely urinary ducts from the 'definitive kidney' until quite close to their common entry into the cloaca. Thus while the urino-genital (Wolffian) duct differs only in size (and function) from the corresponding portion in the female, the ureters proper consist of a series of about twelve C-shaped tubes of gradually decreasing length pursuing a parallel course round the ventro-lateral aspect of the kidney, until they finally enter a very short common duct and pass through the cloacal wall. A comparison between Fig. 72 and Fig. 73 will make this clear. An interesting comparative series (mainly of Japanese Urodeles) has been worked out by Yamagiva (1924) which shows a progressive dissociation of the true ureters from the urino-genital duct during the course of evolution.

The urino-genital duct appears at first sight to be continued forwards beyond the anterior end of the kidney, and in fact this was believed by the older authors (Rathke, Bidder, &c.) to be the case. Leydig (1853) demonstrated the tubular nature of this anterior prolongation, and revealed it as the homologue of the Müllerian duct of the female, although he does not actually call it such.

He however made the mistake of imagining that in both the male and the female the ureters entered Müller's duct some distance anterior to the cloaca. Spengel and Schneider in the year 1876 demonstrated independently that the two ducts remain quite distinct throughout their course, and enter the cloaca by separate orifices. The former author made a careful study of the Müllerian duct in the male, and found that it was traceable, by means of sections, the whole way along the ventral side of the urino-genital duct to the cloaca, where it ended blindly. It normally extends forwards to the point on the posterior wall of the 'diaphragm', where the ostium tubae is situated in the female. It is bound up in a common connective tissue capsule with the urino-genital duct so as to be indistinguishable from it except in sections. It is noteworthy that Müller's duct, and its associated urino-genital duct in the male, are always pigmented, while they never are in the female. The ureters may also bear pigment in the male, but it is usually absent or only very slight. There are no vesiculæ seminales.

2. The Testes.

The *testes* (tes.) are paired and somewhat asymmetrically placed in the abdomen, the right side being slightly anterior to the left. They are suspended by the mesorchia from the mesial edges of the 'sexual kidneys'. Each testis consists of one, two, or three main lobes (usually two), and each lobe is further subdivided by constrictions into two or three zones of different texture and colour, depending on the state of development attained by the sperms within. The lobes of the testis are connected by a narrow strand of genital tissue, while a flagelliform projection of a similar nature extends anteriorly and posteriorly from the corresponding terminal lobes. Meves (1896), as the result of a cytological investigation, distinguishes the following zones in a testis lobe during July or August, i.e. when fully 'ripe'.

(i) The anterior (or posterior) 'flagellum' and the connecting strand, greyish in colour, containing spermatogonia embedded in connective tissue.

(ii) The anterior zone—forming the bulk of the lobe—also grey, containing spermatocytes, and

(iii) a more opaque zone (or sometimes two zones), yellowish or whitish in colour, lying immediately posterior to the spermatocyte zone, containing ripe sperms.

More recently (1922) Humphrey investigated the seasonal development of the testis in an American Urodele and obtained some interesting results which may well be recapitulated here, since they

are doubtless applicable to *Salamandra* or to any other Urodele possessing a multiple testis. The following is a summary of Humphrey's conclusions.

In the young mature male the testis consists of but a single lobe, the multiple lobes being found only in older animals. The residual spermatogonia in the portion of the testis which is emptied in any given year, i.e. zone (iii) above, do not regenerate immediately, but remain dormant for several months, while the functional testis for the ensuing season (zone ii above) develops anterior to the emptied zone. Then supposing the testis at this stage to consist of but a single lobe, the spermatogonia of the posterior 'flagellum' become active and give rise to spermatocytes, thus forming a secondary lobe posterior to the first with the emptied dormant zone forming the connecting strand. This second lobe shifts forwards each season in a similar manner to the first, and eventually a third lobe may be formed posterior to it, but when each lobe reaches the anterior end of the genital tissue it just disappears and leaves the anterior 'flagellum' of dormant spermatogonia. Thus a continual spermatogenic wave moves slowly forwards along the genital strand, and the lobulated appearance is simply the result of this movement combined with the delayed regeneration of the emptied zones.

Spermatogenesis has been investigated by a number of workers, notably von La Vallette St. George (1875), Flemming (1888), Nicolas (1892), von Rath (1893), Rawitz (1895), Meves (1895-6), and Champy (1912). The haploid number of chromosomes is 12 and the diploid 24.

The *sperm* itself has been the subject of investigations by Czermak (1850), von Siebold (1850), and Retzius (1906). Although relatively short when compared with some other Urodeles, e.g. Triton, the sperm of *Salamandra* is long and the nucleus is filiform, while the acrosome is hooked. The middle piece is quite short and of the same diameter as the head. The flagellum bears on one side a crenate membrane along which a sinuous wave is continuously passing, so that it has been called the *undulating membrane*. The tail terminates in a short filiform end piece. The undulating membrane of course provides the means of locomotion.

One hermaphrodite specimen has been described by Feistmantel (1902) in which eggs were found in the testis.

3. The Vasa Efferentia, &c.

The sperms leave the testis through a series (4 or 5) of fine ducts which pass through the mesorchium from the testis to the sexual

kidney. These are the *vasa efferentia* (va.eff.). They do not connect directly with the kidney tubules but enter a fine longitudinal duct which passes right along the mesial edge of the sexual kidney, and very close to it. This duct is in turn connected by a number of very short transverse tubes with the kidney tubules. The longitudinal collecting duct was first described by Bidder (1846) and is consequently called *Bidder's duct* (d.Bd.). According to Spengel the *vasa efferentia* are not ciliated, neither is Bidder's duct nor the connexions with the kidney tubules. The connecting ducts join the Bowman's capsules of the kidney at the pole opposite to that from which the uriniferous tubule leaves. As mentioned above some traces of this system may be found in the female, where of course it is functionless.

4. The Fat-body.

The *fat-bodies* (ft.b.) present no essential difference from those of the female (*q.v.*). They are suspended from the mesorchia mesodorsal to the testes.

5. The Cloaca and its Glands.

The *cloaca* of the male is very different from that of the female, and serves as a ready means for identifying the sexes by external characters, since, in the male, the cloaca is surrounded by a large tubular gland which gives its lips a tumid and swollen appearance, while in the female, where the gland is absent, the opening of the cloaca lies flush with the surrounding skin. The histology of the gland in Triton has been well described by Heidenhain (1890), but it is not easy to correlate his results with the condition in Salamandra, except in a very general way. The cavity of the cloaca is not quite a simple chamber, but is subdivided by infoldings of the wall. Of the diverticula thus produced the most pronounced are a pair of lateral grooves which run in an antero-posterior direction inclined slightly dorso-ventrally. They are somewhat L-shaped in transverse section, and their anterior extremities are expanded into small chambers in which the urino-genital papillae lie. There is further a small ridge-like projection from the antero-ventral wall of the cloacal chamber which may be called the *cloacal papilla* (pap.cl.) (it has sometimes been called the *penis*, but this is a misnomer). It may easily be seen, together with the lateral grooves, by pulling apart the lips of the external opening. The external lips of the cloaca are furrowed by a series (about 15) of elongated pits, while the whole surface of the lateral walls of the chamber, especially ventral to the lateral groove, is thrown into

a series of deep knife-like ridges. These ridges are really composed of a number of long fine papillae amalgamated together, at the apices of which are the openings of the cloacal gland. The ridges are radially arranged with the anterior extremity of the cloaca at the approximate centre. Finally there is a slight median ridge passing along the dorsal wall of the cloaca, which apparently corresponds with the structure labelled *penis* in Heidenhain's figures of Triton, but it is very much less developed in Salamandra.

Histologically the glandular mass is divisible into three portions, called by Heidenhain the pelvic gland, the abdominal gland, and the cloacal gland. Of these the cloacal gland forms by far the largest portion and lies ventrally, i.e. ventral to the lateral diverticula above-mentioned, the abdominal gland lies postero-dorsally, and the pelvic gland antero-dorsally. The abdominal gland is very small and is not easy to distinguish from the pelvic gland, thus contrasting strongly with Triton, where the abdominal gland is well developed.

On removing the skin the *cloacal gland* (= *glandulae ani*, Funk), appears as a heart-shaped structure (gl.cl.) surrounding the cloacal opening, and is seen to consist of a mass of coarse tubules. This expanded ventral portion of the gland is separated from a corresponding dorsal portion (gl.cl.") by the M. caudali-pubo-ischio-tibialis and M. ischio-caudalis, the two parts being connected by a mesial portion alongside the cloacal wall. It discharges its secretion by numerous fine pores situated at the extremities of the long papillae arranged in the cloacal walls as already described, as well as on the cloacal papilla.

The *abdominal and pelvic glands* open on the dorsal cloacal wall. Their tubules are smaller than those of the cloacal gland, and their openings are either flush with the surface or on very low papillae. The most anterior portion of the cloaca, i.e. the portion which adjoins the rectum, consists of a wide tube with folded walls, and its epithelium is ciliated. In addition to the most anterior tubules of the pelvic gland it receives the rectum, the urino-genital ducts, and the bladder. The rectum merges directly into it, while the Wolffian ducts enter it at the apices of a pair of small urino-genital papillae on its dorsal wall (pap.u-g.), situated on either side of the middle line at the anterior end. These openings are relatively farther forwards in the male than in the female, and apparently correspond with the *penis divisus* of Funk. The opening of the bladder is not, as might be expected, at the extreme posterior end of this organ but a short distance anterior to it, and consists of a longitudinal slit in its dorsal wall which opens ventrally into the cloaca immediately opposite the urino-genital papillae (Fig. 71). Thus, although there is no direct

connexion between the ureters and the bladder, the actual distance separating their openings is very small, and the urine, assisted by gravity, would quite naturally tend to flow into the relaxed bladder. The neck of the bladder, the posterior end of the rectum, and the anterior end of the cloaca are, in both sexes, surrounded by a strong fibrous sheath (fbr.sh.), containing smooth muscle elements, which is attached dorsally to the vertebral column and ventrally to the pubo-ischiadic symphysis.

The function of the glands surrounding the cloaca is to secrete mucoid spermatophores which envelop the sperms when they are shed by the male in copulation (see also p. 5). The older anatomists referred to the glands as the 'penis', but they are neither morphologically nor functionally to be compared with this organ. Leydig (1892) and others have sought to homologize the glands with the prostate of Mammals. Certainly there is some functional similarity, but an actual homology is doubtful. The cloacal opening, and indeed the whole gland, is surrounded by smooth muscles so that the tubules may be adequately compressed when their secretion is required.

6. The Urinary Bladder.

The *urinary bladder* presents no essential difference from that of the female (p. 282).

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X

THE DUCTLESS GLANDS

General.

APART from histological considerations, and regarded from a purely anatomical point of view, there is not a great deal to be said relevant to the ductless glands of *Salamandra*. They were first subjected to a detailed investigation in 1888 by Maurer, who studied not only their character and histology in the adult, but also their origin and development. Bolau (1899) undertook a fresh investigation of the histology of the thyroid and thymus of a large number of amphibian types, including *Salamandra*, while Wilder (1929) discussed the significance of the ultimo-branchial body in *Urodeles*. This practically exhausts the anatomical literature of note, but papers dealing with the physiology of the organs concerned are much more numerous.

1. The Thyroid (Thyreoid) Gland (Figs. 37 and 38, gl.thy.).

According to Maurer, the thyroid develops as an unpaired structure which very soon divides into two. It makes its appearance very early in the developing embryo. The thyroid in the adult consists of a pair of elongated ovoid glands about 3.5 mm. long by 1 mm. broad, lying on the floor of the throat at about the level of the os triangulare, immediately in front of the arterial arches, lateral to the MM. genio-hyoideus and rectus cervicis superficialis, and posterior to the M. interhyoideus. Each gland is enclosed in a tough connective tissue capsule into which a few fibres from the M. genio-hyoideus are inserted. The glands are nourished by the thyroid arteries, branches of the external carotids, the blood being returned to the heart by the thyroid veins (p. 226). The hypoglossal nerve crosses the ventral aspect of each gland. Even with the naked eye, or at any rate with a hand lens, each gland is seen to consist of about 20 translucent follicles. The microscopic examination of transverse sections shows that each follicle consists of a single layer of cells which stain very deeply with iron-haematoxylin, and is filled with a clear colloidal fluid, the exact size and appearance of the follicles depending of course on the seasonal and physiological conditions prevailing at the time of fixation.

As is well known, the secretion from the thyroid has a very

important influence over the inception and course of metamorphosis in Amphibia.

2. The Thymus Glands.

The thymus glands are paired from the first, and develop from the dorsal ends of the third, fourth, and fifth gill slits (Maurer). Each gland has therefore a triple origin and frequently presents a trilobed structure in the adult. They are quite large ovoid glands, about 4 mm. long by 3 mm. broad, and are situated laterally on either side of the 'neck' immediately beneath the skin, and about level with the posterior margin of the paratoid cutaneous glands. They are of the 'solid' type of gland, and their cells, which are small, stain intensely with iron-haematoxylin. They are supplied by the cutaneous branch of the systemic arch (p. 201) and drained chiefly by the common facial vein (p. 225). The function of the thymus in Amphibia does not yet seem to be fully understood, but according to Noble (1931), 'the thymus functions in producing lymphocytes, granulocytes, and also erythrocytes to a certain extent'. It is apparently stimulated by thyroid feeding.

3. The Parathyroids (Epithelial Bodies) (Fig. 38, ep.).

These bodies are also derivatives of the visceral clefts, notably the third and fourth, but of their ventral ends. They are easily seen in dissecting, lying lateral to the arterial arches immediately ventral to the thymus, and consist of a pair of small spherical bodies on either side. They are highly vascular and are usually supplied by small twigs direct from the arterial arches. They appear late in larval life and apparently have the same function in Amphibia as in Mammals, namely to control the concentration of calcium salts in the blood (Waggener, 1929). They are widely separated from, and have no connexion with, the thyroids, although there is experimental evidence to show that the removal of the thyroids in toads causes a corresponding hypertrophy of the parathyroids.

4. The Ultimo-branchial Body.

This structure has also been variously termed *post-branchial body*, *supra-pericardial body*, and *ultimo-branchial body*. The last name has been adopted since it best indicates the origin of the structure from the sixth gill-slit. In the adult Salamander it normally occurs on the left side only, although in the Anura it is a bilateral structure. It is quite small and is best observed in sections, where it may be seen lying ventral to the M. cephalo-dorso-subpharyngeus and mesial to

the M. rectus cervicis profundus, in the angle formed by these two muscles, at the level of the truncus arteriosus. It presents, when stained with iron-haematoxylin, a very similar appearance to the thyroid gland, but consists of only about two or three small follicles. From the study of this body in a large series of Urodeles, Wilder (1929) came to the conclusion that, owing to its extreme variability, it could have little or no physiological importance.

5. Other Glands.

Adrenal bodies are present and may be seen as a series of orange patches along the ventro-mesial borders of the kidneys. They are also to be found anterior to these organs, even as far forwards as the subclavian artery, and they are then associated with the sympathetic ganglia (see also pp. 179, 182, and 278).

The *pineal organ* and *pituitary body* are described in the section dealing with the brain (pp. 129 and 130). The *spleen*, although a ductless gland, is described on p. 267, together with the alimentary canal. The *pancreas*, *liver*, and *gonads* have also endocrine functions although they can hardly be considered as 'ductless glands'.

BIBLIOGRAPHY OF SECTION X

70, 273, 274, 285, 286, 375, 419, 420, 452, 453, 527, 612, 742, 800.

XI

THE SKIN AND SENSE ORGANS

THE SKIN

1. General.

THE outer skin of the Salamander is moist and devoid of scales. It is highly glandular, however, and the glands are of two kinds—the *mucus glands*, whose function is to keep the skin moist, and the *venom glands*. In this respect the skin of *Salamandra* is less slimy than that of the Frog, a feature probably correlated with the diminished respiratory function of the skin in the former animal. The mucus glands are distributed over the whole surface, and do not disclose their presence by any external excrescence or other sign visible to the naked eye.

2. Venom Glands.

The second kind of gland is the *poison* or *venom gland*. These are much larger than the mucus variety, and usually reveal their location by a slight mammilliform protuberance, while the central pore is quite visible to the naked eye, and where the glands occur beneath the yellow pigment—as is frequently the case—the opening is often marked by a black dot. Although the venom glands may occur almost anywhere on the body, they are more numerous over the dorsal surface, and are more highly developed in certain definite areas as in the *paratoid glands* and along the mid-dorsal line from the nape to the tip of the tail. There are also, strangely enough, several medium-sized glands on the feet between the toes. The *paratoid glands* consist of some twenty-five to thirty flask-shaped glands, the bases of which may readily be seen on removing the skin. A double alternating row of such glands extends right along the back for the whole length of the vertebral column. The remaining scattered venom glands are definitely smaller and less conspicuous. The venom glands are distinguishable from the mucus variety, particularly in preserved specimens, by their more granular contents and opaque appearance, the mucus glands being translucent or pearly.

With regard to the histology and development of the glands much has been published which is outside the scope of the present work. For these details the papers of Leydig (1876), Pfützner (1880), Drasch (1894), Ansel (1900-2), Schuberg (1908), Nierenstein

(1908), and Theis (1932) may be consulted. Ancel showed that the poison glands were of ectodermic origin, while Nierenstein held that they arose secondarily from degenerating mucus glands, a view with which Esterly—for *Plethodon*—agrees. Recently, however, Theis has reinvestigated the whole question and concludes that there is *no transition from mucus to poison glands*.

When a Salamander is irritated, e.g. by chloroform, a white milky fluid is seen to exude from the venom glands. This substance is a fairly potent irritant poison and eventually causes paralysis in the victim. Although there is no mechanism whereby the animal can inject the poison into a victim, and it must therefore remain a purely defensive weapon, nevertheless the Salamander can, on occasion, squirt or spray the fluid to a surprising distance, quite sufficient to get into the eyes and nose of a too inquisitive marauder. Probably this action is effected by means of the smooth muscle elements which invest the glands (cf. also Esterly, 1904).

3. Venom.

A fairly considerable amount of work has been carried out in an endeavour to elucidate the chemical nature of the poison, and two alkaloids have been isolated from it in a pure state. The first worker in this field was Zalesky (1866) who isolated the chlorhydrate of one of them, which he called *Samandarin*, and suggested for it the formula $C_{68}H_{66}O_{10}N_2$. His choice of name was due to a suggestion by Prof. Roth of Tübingen that the Greek word *σαλαμάνδρα* comes from the Persian *Samandar*, a similar word occurring in both Arabic and Hindustani. Zalesky also investigated its physiological effects. The next worker was Faust (1898 and 1900) who isolated the sulphate of both alkaloids. To *Samandarin sulphate* he gave the formula $C_{52}H_{80}N_4O_2 + H_2SO_4$ or $(C_{26}H_{40}N_2O)_2 + H_2SO_4$. The second base he named *Samandarinidin* and suggested the formula $(C_{20}H_{31}NO)_2 + H_2SO_4$ for its sulphate. He supposed that they were both built around the methyl pyridin group $C_5H_5(CH_3)N$ and that *Samandarin* has more of these groups than *Samandarinidin*. He also found that the pharmacological strength of the former was 7–8 times greater than that of the latter. Gessner (1926), and Gessner and Craemer (1930) have recently made a fresh analysis of the Salamander venom and have isolated both substances in the pure state. Their analysis of *Samandarinidin* does not quite agree with that of Faust, having one atom of carbon less and one atom of oxygen more than his, namely, $C_{19}H_{31}O_2N$, with a freezing point of $187^\circ C$.

It is not proposed to catalogue the numerous pharmacological and

physiological experiments which have been carried out with these substances. They are fully described in the papers mentioned.

THE SENSE ORGANS

I. THE EAR.

1. General.

The auditory apparatus of Urodeles consists, as in all higher vertebrates, of a membranous labyrinth of ectodermal origin for the combined functions of balancing the body and the perception of sounds, together with certain skeletal elements modified for the purpose of conveying the auditory stimuli from the external medium to the labyrinth. These two distinct portions have each been the subject of separate investigations by the various workers dealing with the organ of hearing, and accordingly they will also be dealt with separately here.

2. Skeletal Structures.

The *skeletal* portion is the more highly specialized and is very characteristic of the group.

The earlier authors dealing with the ear of the Salamander, as well as those investigating the structure of the skull in general, recognized only one skeletal element within the fenestra vestibuli (ovalis), namely the operculum. The first investigator to recognize the homologies of all the skeletal parts concerned and to give an adequate account of their relations was Gaupp (1898), but their full significance and mode of operation were not completely understood until the investigations of Kingsbury and Reed (1902-20).

It is perhaps almost unnecessary to point out that the familiar tympanum and tympanic cavity of the Frog are wanting in Salamandra, or for that matter in all Urodeles. Nevertheless a *columella* is present, but it remains quite vestigial and does not reach the outer surface, and is apparently *functionless in terrestrial adults*. There is a considerable amount of variation among the several families of Urodeles, and these differences have been used for classificatory purposes by Reed (1909 and 1920), although Dunn (1923) questions their value in this respect. It is unnecessary to go into the question in detail here, but the reader may refer, either to the original papers quoted, or to the summary given by Goodrich (1930, p. 480).

In the Salamander there are two structures filling the *fenestra vestibuli* (ovalis) of the auditory capsule—(i) the *columella*, which is extra-otic in origin, and (ii) the *operculum*, a cartilaginous plate cut

out from the walls of the ear capsule. The former is the functional element in the larva, and the latter in the adult.

The *columella* develops in a ligament, the *suspensor-stapedial ligament*, stretching from the membrane of the fenestra to the proximal end of the quadrate and squamosal. It consists of two portions—first a short rod-like stylus connecting the suspensorium (squamosal and quadrate) with the second portion—a flat plate-like expansion filling the anterior portion of the fenestra. In the adult Salamander the columella is ossified and fuses with the wall of the auditory capsule so as to be scarcely distinguishable from it.

The *operculum* (fig. 2, c.op.) fills the remainder of the fenestra vestibuli. It is a plate of cartilage, approximately circular in plan, and shaped like a very thick crescent in transverse section. It is attached to the auditory capsule at its edges by the membrane of the fenestra, and thus lies entirely free from other skeletal parts, being supported by an elastic membrane only. As already mentioned it develops from the wall of the ear capsule, but it is perhaps questionable whether it is 'cut out', as it were, by absorption of the tissue round it, or whether it arises by an extension of cartilage into the membrane closing the fenestra. It appears probable that the latter is the chief process at work. The *operculum* is attached to the *supra-scapula* by a strap-like muscle derived from the *M. levator scapulae*, and called by Gaupp *M. opercularis*. The presence of this muscle is at first sight rather extraordinary, and it is absent in those forms, e.g. *Necturus*, which lead an entirely aquatic existence in both larval and adult phases. In such forms also the columella is *free* from the auditory capsule but *fused* with the operculum, and it is supposed that in aquatic forms, both larvae and adults, the auditory stimuli reach the ear from the external medium—water—by means of the following path:—jaws, suspensorium, columella, fenestra. Such forms, particularly when adult, are much given to resting the whole of the body, including the jaws, on the bottom, and the lower jaw is thus in a favourable position for receiving vibrations directly from the ground. Now in terrestrial forms, e.g. *Salamandra*, the head is always kept well clear of the ground, and, since it is manifestly impossible for the vibrations of a rare medium like air to affect so heavy a skeletal structure as the jaws, the auditory stimulus must travel by some alternative route in these animals. This route is by means of the fore-limbs to the scapula and suprascapula, and from thence to the operculum *via the M. opercularis*. In this connexion it is interesting to note that Dunn (1922) gives a description of a primitive Urodele—*Hynobius leechi*—in which the columella is free from the auditory capsule, and there is in

addition a M. opercularis joining the operculum to the shoulder, whereas in almost all higher forms either one or other *alone* is present.

The 'hearing' of Urodeles must obviously be confined to the perception of a very small range of low-frequency vibrations of wide amplitude, but it is possible that the M. opercularis may have the effect of increasing the range somewhat, since, being a striped muscle, its tension is capable of adjustment by the animal.

3. The Membranous Labyrinth (Pl. XXIV, figs. 80 and 81).

Apart from the earlier workers (e.g. Scarpa, Pohl, Huschke, Windischmann, &c.) the first investigator to make a really detailed study of the membranous labyrinth of Amphibia was Hasse (1873). He was succeeded by Kuhn (1880), whose paper was, in turn, closely followed in the next year (1881) by the well-known work of Retzius. All these authors give excellent descriptions of the ear of *Salamandra* and are, in the main, correct. They all fall into the same error in imagining that the *ductus perilymphaticus* communicates with the epicerebral space—a mistake which was corrected later by O'Neill, Sterzi, Harrison, &c. Both Hasse and Kuhn imagined that the *pars neglecta* (their *pars initialis*) was the anlage of the cochlea of mammals, but Retzius did not share this view, and to him is due the name *pars neglecta*. Both the earlier authors describe a *pars basilaris* supported by a 'cartilaginous' frame (Knorpelrahmen). Retzius denies the existence of both a *pars basilaris* and a 'Knorpelrahmen'. In this, however, he is himself in error (as Harrison (1902) showed), and the earlier authors were right. Both Kuhn and Retzius deal with the microscopic structure of the maculae, &c.

The membranous labyrinth of *Salamandra* is fairly typical of Urodeles in general, but differs in several points from that found in Anura, e.g. the Frog. After clearing away the muscles arising from the auditory capsule the ridges over the semicircular canals may be clearly seen. In order to remove the labyrinth from the capsule—not a particularly difficult operation—it is advisable to decalcify the skull by immersing it in sulphurous acid. The roof of the capsule may then easily be cut away. Care must be taken with the *anterior septum semicirculare* (a bony pillar joining the roof to the ventro-mesial wall of the capsule), which lies just posterior to the anterior semicircular canal, and serves to separate this canal from the main cavity. The other two septa, related in the same way to the other semicircular canals, are rarely complete, so they do not usually give trouble.

Compared with the size of the skull as a whole the ear is large and flat, and, in most places, is well separated from the bony capsule.

The older authors (Hasse, Kuhn, and Retzius) imagined that this space contained perilymph, and that the labyrinth simply floated free in this fluid supported by a few strands of connective tissue. Harrison (1902) showed that this was not the case and that the perilymph was restricted to certain definite regions (see below), while the remaining space between the labyrinth and the capsule was occupied by a tissue which he termed *perilymphatic tissue*. This is a connective tissue which becomes specially dense, 'almost cartilaginous', around the labyrinth itself.

The following may be termed the 'intrinsic' portions of the ear—three *semicircular canals* with their *ampullae*, the *utricle*, the *sacculus*, the *lagena*, *pars basilaris* and *pars neglecta*, and the *ductus endolymphaticus*. The 'extrinsic' portions are the *perilymph system* and the *sacculus endolymphaticus*.

The *semicircular canals* are not all equal in extent or in curvature. The shortest, and at the same time the most nearly circular, is the *posterior canal* (can.s.p.). It lies in a vertical plane pointing in a postero-lateral direction relative to the axis of the body. It may be supposed to arise from the *pars superior utriculi* just behind the anterior canal, and, after completing almost an entire circle, it re-enters the *utricle* at the *pars posterior* just below the origin of the horizontal canal. Its *ampulla* is situated at the ventral end (amp.p.).

The *horizontal canal* (can.s.h.) (or *canalis externus*, Kuhn) arises from the *pars posterior utriculi* between the two ends of the posterior canal. The curvature is not quite even throughout its length. The posterior portion describes roughly the quadrant of a circle and is then succeeded by a more flattened mesial portion. Finally the anterior end bends round more sharply again and enters the *recessus utriculi* close to the anterior canal. It does not lie in a truly horizontal plane relative to the other canals, but is slightly depressed anteriorly. The *ampulla* is at the anterior end (amp.h.).

The *anterior canal* (can.s.a.) arises from the *sinus superior utriculi* close to the posterior canal, and lies in a vertical plane pointing in an antero-lateral direction. It remains almost flat for about two-thirds of its length and then bends sharply ventralwards to enter the dorsal aspect of the *recessus utriculi*. The *ampulla* is at the anterior end (amp.a.).

The *utricle* is a wide tube, more or less saddle-shaped, sitting over the mesial part of the sacculus. Its most dorsal portion, the broad *sinus superior* (s.s.utric.), gives rise to the anterior and posterior canals, while its anterior end dips ventralwards to the *recessus utriculi* (rec.utric.), which is the expanded portion into which the ampullae

of the anterior and horizontal canals open. Posteriorly the utriculus also turns ventrally into the *sinus posterior*, which is continued into the ampulla of the posterior canal. The utriculus further communicates, by means of an oval opening, with the *sacculus*. This opening, the *canalis utriculo-saccularis* (can.utric-sac.), is situated at the base of the utriculus below the sinus superior, and from its mesial wall the *pars neglecta* (p.neg.) (Retzius) is evaginated.

The *sacculus* (sac.) is a lens-shaped sac, compressed in a ventro-mesial plane. It contains otolith granules and communicates with the *sacculus endolymphaticus* by means of the endolymphatic duct (d.el.). It also opens into the *utriculus*, as already noted, and into the *lagena* and *pars basilaris*. The lateral wall is extremely thin and separates the sacculus from the main perilymphatic space—the *spatium sacculare*. The *ductus endolymphaticus* (d.el.) arises from the dorso-mesial aspect of the sacculus close to the *canalis utriculo-saccularis* and passes directly dorsalwards, mesial to the utriculus and close to its wall, and directly between the origins of the two vertical canals. At about the level of the dorsal margin of the sinus superior utriculi the duct passes through the *foramen endolymphaticum* into the cranial cavity, where it expands into the *sacculus endolymphaticus* (see 'Membranes of the Brain', p. 121 et seq.).

The *lagena* (lag.) (or *lagena cochleae*, Retzius) is a somewhat pear-shaped pocket opening from the mesial aspect of the sacculus near its posterior margin. It contains an otolith.

The *pars basilaris* (p.bas.). Although both Hasse and Kuhn had correctly described the *pars basilaris* in *Salamandra*, yet Retzius (1881) denied its existence as a separate recess, and supposed it to be represented by a small oval nerve-ending on the inner wall of the upper end of the lagena. Harrison (1902) corrected this error in favour of the older authors—a result which is here confirmed. The *pars basilaris* is a small evagination from the dorso-mesial wall of the *lagena* facing the opening of the latter into the *sacculus*.

4. Nerve-endings.

The ear is supplied by the eighth cranial nerve. The fibres of this nerve terminate on plate-like areas of sensory cells, called *maculae*, which occur at the following positions—at the ampullae of the semicircular canals, here called *cristae* by Retzius, on the floor of the *recessus utriculi*, the *sacculus*, the *pars neglecta*, *pars basilaris*, and the *lagena*.

The *cristae acusticae ampullorum* (Retzius) are bi-concave areas lying on the ventral surfaces of the posterior and horizontal ampullae, and on the anterior face of the anterior vertical ampulla.

The *macula acustica recessus utriculi* (Retzius) lies on the floor of the recessus utriculi and, together with the two anterior (horizontal and vertical) ampullae, it is innervated by the ramus anterior of N. acusticus.

The *macula acustica sacculi* (Retzius) is the largest of all the sensory plates and covers the mesial wall of the sacculus and is supplied by the *ramus medianus*, N. *acusticus*.

The *macula acustica neglecta* lies on the dorsal wall of the *pars neglecta*, while the sensory area of the *pars basilaris* practically surrounds that part of the labyrinth, and that of the *lagena* is confined to its mesial wall. The last three maculae mentioned, together with the crista acustica of the posterior ampulla, are supplied by the ramus posterior of the auditory nerve. The histology of the maculae, &c., has been well described by Kuhn and Retzius from osmic acid preparations. Briefly the maculae consist of a superficial layer of cylindrical cells with sensory hair-like processes, supported by round basal cells.

5. The Perilymphatic System.

The correct elucidation of the extent and relations of this system is due to Harrison (1902). His terminology is therefore used here. Within the ear capsule the largest space containing perilymph is the *spatium sacculare*. This large sac lies lateral to the sacculus and mainly ventral to the horizontal canal, and fills the whole lateral half of the capsule. It lies in close apposition to the membrane closing the fenestra vestibulae, and to the operculum. The wall separating this space from the sacculus is exceedingly thin.

Leaving the *spatium sacculare* posteriorly, on its dorso-lateral aspect is the *ductus perilymphaticus* (d.pl.), a fairly wide tube only slightly smaller in diameter than the semi-circular canals. The ductus passes mesialwards around the posterior end of the labyrinth and lies ventral and lateral to the posterior end of the horizontal canal, mesial to the posterior canal and the sinus posterior of the utriculus, finally emerging on the mesial aspect of the labyrinth, dorsal to the lagena and pars basilaris, and ventral to the pars neglecta. It then dips ventralwards and enters the cranial cavity through the *apertura ductus perilymphatici* (O'Neill) (the *foramen rotundum* of Hasse), in the mesial wall of the otic capsule. Within the cranium the duct expands into a comparatively small sac—the *saccus perilymphaticus* (or *spatium meningeale*, Harrison). See also p. 126.

There are two small outgrowths from the ductus perilymphaticus within the ear capsule. These occur just proximal to the point where

the duct enters the cranium. The first has been called the *recessus partis neglecta* by Harrison who first described it. It is a short wide diverticulum which comes into intimate contact with the ventral wall of the pars neglecta, the separating wall being exceedingly thin. The second diverticulum is smaller and is the *recessus partis basilaris* of Harrison. It bears a similar relation to the pars basilaris.

These three areas, at the pars neglecta, pars basilaris, and sacculus, where the membrane separating the perilymph from the endolymph is extremely thin, are spoken of by Harrison as 'tympanal areas', and it is, he supposes, through these areas, and through them alone, that the vibrations imparted to the perilymph by the operculum are transmitted to the endolymph. By these vibrations the otolith crystals in the sacculus and lagena are set in motion, and these in turn affect the sensory 'hairs' on the surface of the cells covering the maculae acusticae, and thus the auditory nerve is stimulated. The function of the *sacculus endolymphaticus* within the cranial cavity is presumably similar to that of the foramen rotundum of the mammalian ear, namely to act as a buffer for the vibrations of the perilymph.

II. THE EYE

1. General.

The eye of the Salamander is relatively large and stands up prominently from the surface of the head. The *bulbus oculi* is nearly spherical, and, in the larva, is protected by a scleral ring of cartilage which, however, disappears at metamorphosis so as to leave no trace in the adult. The lens is also nearly, but not quite, spherical. According to Beer (1899) accommodation is not effected by a change in the curvature of the lens but by an alteration in its position, since he finds that it moves towards the iris on stimulation. This movement is brought about by a ciliary muscle which constricts the back chamber and so forces the lens out, while the iris is said to play a small but unimportant part.

Klingelhöffer (1910-11) shows that the refractive index of the Amphibian eye in general is such that it is a little long-sighted in water, and that the lens, being less truly spherical than that of the fish, and possessing some slight capacity for accommodation, is truly intermediate between an aquatic and an aerial structure.

Johnson (1926) during the course of an ophthalmological investigation of Amphibian and Reptilian eyes found that *Salamandra maculosa* exhibits the simplest and apparently the most primitive condition of the disc.¹ It is quite round and very small, being only

¹ The point of entry of the optic nerve, E.T.B.F.

one-third or one-quarter that of the majority of the Anura. It is dull white in colour and is not covered by anything, nor is there pigment nor differentiation of any kind, nor the slightest trace of any vessels, either hyaloidean or discoidal.' In this last feature *Salamandra* differs markedly from the Frog. Another difference between these two animals lies in the absence, in the Salamander, of any trace of the vertical pigmented stripe which extends from the lower edge of the pupil to the margin of the iris in the Anura. Johnson supposes that this stripe, which is always associated with a groove and which sometimes extends to the upper portion of the iris also, is the result of the mechanical strain of the iris muscles, and is phylogenetically the oldest condition, and that the round pupil of the Salamander represents the highest stage of development. The same author finds considerable accommodating powers, but no movement of the eye itself other than that of retraction. This last feature is not surprising in view of the relatively weak development of the ocular muscles other than *M. retractor bulbi*.

Quite recently Dr. Ida C. Mann (1931) has made an exhaustive comparative study of the iris pattern in vertebrates, and notes that in the Salamander the arteries enter the iris from below and on the temporal side, while in some specimens the inferior iris artery is a branch of the temporal and does not enter separately. This latter she thinks is the more typical Urodele arrangement. The arteries break up irregularly round the pupil and the blood drains away by a few radial veins, not definitely superficial to the arteries and not arranged with anything like the regularity found in Reptiles. The pigmentation of the iris is entirely brown.

2. Glands of the Orbit.

Apart from histological details there is not much that can be added concerning the structure of the eye itself. It is supplied by a pair of ciliary nerves, a superior (p. 140) and an inferior (p. 140), while the *bulbus oculi* is attached to the wall of the skull by a strong fibrous sheath surrounding the *optic nerve*, the whole forming the *optic peduncle*. Within the orbit, beneath the *bulbus oculi*, is a mass of glandular tissue which shows a tendency to become differentiated into two sections. The anterior region is the *Harderian gland*, and the posterior the *lacrimal gland*. In *Salamandra* the separation of the Harderian portion in the anterior angle of the orbit from the remainder of the gland may be partial or complete. In Triton there is no such separation (Sardemann, 1887). Hence this animal may be regarded as exemplifying the primitive condition, while the Salamander shows,

by comparison, that the Harderian and lacrimal glands have arisen by differentiation from a common glandular mass.

The *naso-lacrimal duct* runs from the anterior corner of the eye to the nasal cavity passing beneath the pre-frontal bone in so doing.

3. The Eyelids.

The upper eyelid is the larger and is movable, as it is in the whole family Salamandridae. The lower lid, according to Johnson, is probably homologous with the *membrana nictitans* of higher vertebrates, the true lower lid of these animals arising as a cutaneous fold external to it, only a slight trace of this fold being detectable in the Salamander. Both upper and lower lids are moved by means of a tendon attached to the *M. retractor bulbi* and they are therefore closed synchronously with the retraction of the eye-ball (cf. p. 51). In addition to this mechanism there are a few smooth muscle elements in the upper eyelid so that it is apparently capable of some independent movement.

III. THE NOSE

1. General.

The olfactory passages of the Salamander are relatively large chambers situated within the nasal capsules. With the exception of a small area around the external openings they are completely protected by the skeleton. Two distinct regions are distinguishable in each olfactory chamber, namely, the main chamber, or *cavum nasi*, which is shaped like a flattened ovoid, from which protrudes a lateral gutter-like diverticulum—the *sinus lateralis nasi*. Into this lateral gutter the *ductus naso-lacrimalis* opens, while the external narial opening is situated just mesial to its anterior end. The *sinus lateralis nasi* is lined by ciliated epithelium, but not the main *cavum nasi*.

2. Jacobson's Organ.

In 1895 Seydel suggested that *Jacobson's organ* occurred in the sinus lateralis, and named the gland lying just mesial to it, beneath the cavum nasi, *Jacobson's gland*. In 1898 Mihalkovics opposed this view on the ground that, in all other vertebrates which possess a Jacobson's organ (including the Frog), this structure is found *mesial* to the posterior nares and *not lateral* to them. He therefore concludes that a true Jacobson's organ is absent in Salamandra, but agrees that the *sinus lateralis nasi*—his *recessus maxillaris*—has a similar function, namely that of testing the expired current, and he therefore regards

it as *analogous to* but not *homologous with* a true Jacobson's organ. Three years later, in 1901, Hinsberg studied the development of the nasal capsule in Triton and came to the conclusion that, in that animal, a patch of sensory epithelium, homologous with Jacobson's organ, arises mesially and shifts to a position lateral to the internal nares *before* this opening develops. Thus he maintains that the lateral position is a specialization of the Urodela, but that nevertheless the homology is true. Zuckerkandl (1910) agrees in the main but concludes, on the grounds of its nerve supply, that the Jacobson's organ of Urodeles cannot be homologous with that of the Amniota. Bruner (1914) agrees with Seydel as to the location of Jacobson's organ, while Herrick (1914), also on neurological grounds, doubts the existence of this structure in the Urodela, but says that in Anura it has assumed a definitive form as a diverticulum from the *mesial* side of the nasal sac, with its characteristic innervation by the vomero-nasal nerve. Von Navratil (1926) does not agree with Seydel's identification of the *sinus lateralis nasi* with the organ of Jacobson on morphological grounds, but thinks that Seydel's sensory epithelium may become the sinus maxillaris. In 1927 Kurepina investigated the development of the primary choanae in Urodeles (Triton) and arrived at conclusions diametrically opposed to those of Hinsberg. He claims the existence of a primary oro-nasal groove between the nose and mouth, and hence there can be no lateral shifting of Jacobson's organ such as Hinsberg describes.

Thus, while it still remains a somewhat doubtful question, there is evidently a growing consensus of opinion among morphological embryologists against Seydel's view, and in favour of the absence of Jacobson's organ in Urodela. The absence of a vomero-nasal nerve may perhaps be taken as the deciding factor. It is generally agreed however that the sinus lateralis nasi is the *functional equivalent* of the Amniote organ of Jacobson, i.e. that it is used for testing the exhalent current.

3. Opening and Closing Mechanism.

Another region of special interest in the nasal organ is the apparatus for opening and closing the external nares. This was discovered and described by Bruner (1896 and 1901) and consists of a set of three smooth muscles, one constrictor and two dilators. There is no cartilaginous support to the edge of the narial opening as there is in the Frog. The opening in the cartilaginous nasal capsule, in which each external naris lies, is very much larger than the actual cutaneous opening, and houses the muscular apparatus as well.

It is the *fenestra narina* (Stadtmüller) or *fenestra rostro-nasalis* (Bruner) (Pl. XXIV, fig. 82).

The *M. constrictor naris* (m.c.n.) (Bruner) bounds the posterior edge of the narial opening for rather more than a semicircle, its ends being inserted on the anterior wall of the fenestra on the *cart. cupullaris*.

The *M. dilatator naris* (m.d.n.) (Bruner) arises from the posterior border of the fenestra narina, i.e. from the *cart. retro-narina*, and passes directly forwards to the posterior border of the external naris, deep to the constrictor muscle. It is inserted on the cutaneous wall of the narial opening.

M. dilatator naris accessorius (m.d.n'.) (Bruner) is an obliquely directed muscle. It arises from the lateral border of the fenestra narina, partly from the cartilage and partly from the maxilla. The muscle passes obliquely antero-mesially and is inserted in the posterolateral margin of the narial opening, deep to, and amongst, the lateral fibres of the *M. constrictor naris*.

In his later paper (1901) Bruner further showed that the relation of the nasal muscles to the nasal gland, the *glandula nasalis externa*, is such as to force the secretion from the gland simultaneously with the closing of the nasal opening. He also showed that they arise *in situ* from the mesoderm and are not derived from any other muscles.

The *internal nares* are large and unprotected by valves.

The *glands of the nasal capsule* may be reckoned as consisting of two masses, one external and one internal. The *glandula nasalis externa* has already been mentioned. It is situated above the sinus lateralis nasi within the fenestra narina in close proximity to the external naris, and to the opening of the ductus naso-lacimalis into the nasal capsule (d.nas-lc.). As described above it is compressed by the *M. constrictor naris*, so that its function would seem to be that of keeping the edges of the external narial opening moist. The *glandula nasalis interna* practically envelops the cavum nasi, and lies entirely within the nasal capsule. Its function is to keep the olfactory epithelium moist. As mentioned above Seydel distinguishes the ventral portion as *Jacobson's gland*.

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INDEX

NOTE. All blood-vessels, nerves, and muscles have been indexed under their Latin names regardless of whether they have been referred to in the text by the Latin or English terminology. Thus, all references to the peroneal nerve will be found under *Nervus peroneus*, and those to the vertebral vein under *Vena vertebralis*, while certain of the more familiar terms have been listed under both systems, so that, for example, the subclavian artery will be found under *Arteria subclavia* and also by its English name under the letter 'S'.

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ABBREVIATIONS USED IN PLATES

(N.B.—Where the terminal twig of a nerve or blood-vessel in Plates X—XVI inclusive supplies a definite muscle it is labelled with the abbreviation for the muscle *without* the prefix 'm'. Thus the nerve supplying the ischio-caudalis muscle, m.is.cd., is labelled is.cd., and so on.)

A.III. carotid arch.	a.na.l. arteria nasalis lateralis.
A.IV. systemic arch.	a.na.p. " " posterior.
A.V. 'third' arch.	a.o.i. " " orbitalis inferior.
A.VI. pulmonary arch.	a.o.s. " " superior.
a.alv. arteria alveolaris.	a.o.na. " " orbito-nasalis.
a.aud. " " auditiva.	a.ob. " " obturatoria.
a.b. " " basilaris.	a.oes.d. " " oesophagea dorsalis.
a.br. " " brachialis.	a.oes.v. " " ventralis.
a.car.ce. " " carotis cerebialis.	a.od.1 " " oviducalis anterior.
a.car.e. " " " externa.	a.od.2 " " " medialis.
a.car.i. " " " interna.	a.od.3 " " " posterior.
a.cd. " " caudalis.	a.o.ph. " " ophthalmica.
a.ce.a. " " carotis cerebialis, ramus anterior.	a.o.ph.s.a. " " " superior anterior.
a.ce.v. arteria cerebialis ventralis.	a.o.ph.s.p. arteria ophthalmica superior posterior.
a.circ.sc. " " circumflexa scapulae.	a.pal.a. arteria palatina anterior.
a.cl.l. " " cloacae lateralis.	a.pal.nas. " " palato-nasalis.
a.cl.m. " " cloacae medialis.	a.pect. " " pectoralis.
a.d-h. " " duodeno-hepatica.	a.pet.l. " " petrosa lateralis.
a.d-lum. " " dorso-lumbalis.	a.pf.br. " " profunda brachii.
a.d-pan. " " duodeno-pancreatica.	a.ph. " " pharyngea.
a.e.a. " " epigastrica anterior.	a.ph.asc. " " pharyngea ascendens.
a.e.p. " " " posterior.	a.pt. " " pterygoidea.
a.fem. " " femoralis.	a.pud. " " pudenda.
a.g.a. " " gastrica anterior.	a.pul. " " pulmonalis.
a.g.lien. " " gastrico-lienalis.	a.r. " " renalis.
a.gen.s. " " genitalis sinister.	a.r.s. " " " superficialis.
a.gl. " " glutea.	a.s.sc. " " subscapularis.
a.hym. " " hyomandibularis.	a.scl. " " subclavia.
a.il.com. " " iliaca communis.	a.subl. " " sublingualis.
a.is. " " ischiadica.	a.sup.cor. " " supracoracoidea.
a.lab. " " labialis.	a.t. " " temporalis.
a.ling. " " lingualis.	a.th. " " thoracica.
a.m. " " mandibularis.	a.tr. " " trapezia.
a.m.e. " " " externa.	a.vert. " " vertebralis.
a.m.i. " " " interna.	a.ves. " " vesicalis.
a.max.a. " " maxillaris anterior.	ac. acetabulum.
a.max.m. " " " medialis.	ad.b. adrenal bodies.
a.max.pal. " " maxillo-palatina.	ad.ly.sv. vessel joining the subvertebral and lateral lymphatic trunks.
a.mes.a. " " mesenterica anterior.	
a.mes.p. " " " posterior.	

- ad.s.ly.sc.' junction with the subscapular lymph sinus (pars ventralis).
 ad.s.ly.ing. junction with inguinal lymph sinus.
 amp.a. anterior ampulla.
 amp.h. horizontal ampulla.
 amp.p. posterior „
 an. anus.
 an.pet.l. antrum petrosus laterale.
 ap.d.el. opening of the endolymphatic duct into the sacculus.
 aur. auricle.
 aur.d. right auricle.
 aur.s. left auricle.
 b.c. bulbus cordis.
 bl. bladder.
 c.a.or. antorbital cartilage.
 c.ary. arytenoid cartilage.
 c.c.hy. cerato-hyal.
 c.c.br.i cerato-branchial 1.
 c.col.eth. columella ethmoidalis.
 c.cop. copula.
 c.cor. coracoid.
 c.cr.rs. crista retrosellaris.
 c.cup. cartilago cupularis.
 c.ec.ch. cartilago ectochoanal.
 c.h.br.i hypobranchial 1.
 c.h.br.ii hypobranchial 2.
 c.h.hy. hypo-hyal (first radial of the copula).
 c.hyp.com. hypochordal commissure.
 c.M. Meckel's cartilage.
 c.obl. cartilago obliqua.
 c.op. operculum.
 c.p-q. palato-quadrate.
 c.pb. pubis.
 c.pl.con. planum conchale.
 c.pl.in. „ internasale.
 c.pr.cor. procoracoid.
 c.pr.h. cartilago prehallucis.
 c.pr.p. „ prepollicis.
 c.pt. cartilaginous pterygoid.
 c.r. rostrum pre-nasale.
 c.rad. posterior radial of the copula.
 c.rd. radiale.
 c.rt.nar. cartilago retro-narina.
 c.sc. suprascapula.
 c.t. tibiale.
 c.t.in. tectum internasale.
 c.t.syn. „ synoticum.
 ca.in. cavum internasale.
 can.car. carotid canal.
 can.h. haemal canal.
 can.nl. neural canal.
 can.s.a. anterior semicircular canal.
 can.s.h. horizontal „ „
 can.s.p. posterior „ „
 can.utric-sac. utriculo-saccular canal.
 can.va. vertebral arterial canal.
 ce.h. cerebral hemispheres.
 cen. centrum.
 cerb. cerebellum.
 co.f. fibular condyle.
 co.l.h. epicondylus lateralis humeri.
 co.m.h. „ medialis „
 co.oc. occipital condyle.
 co.r. radial condyle.
 co.t. tibial condyle.
 co.u. ulnar condyle.
 col. columella.
 com.a. anterior commissure.
 com.c. corpus callosum.
 com.ha. habenular commissure.
 com.p. posterior commissure.
 com.ves. communicating vessel.
 cr.d.h. crista dorsalis humeri.
 cr.m. crista muscularis.
 cr.tb. „ tibialis.
 cr.v.h. „ ventralis humeri.
 ct.ly.h. central lymph heart.
 cut. skin—also any unnamed twigs of nerves or blood-vessels supplying it.
 d.a. dorsal aorta.
 d.B. ductus Botalli.
 d.Bd. Bidder's duct.
 d.c. common bile-duct.
 d.C. duct of Cuvier.
 d.C.d. right duct of Cuvier.
 d.C.s. left „ „
 d.cy. cystic duct.
 d.el. endolymphatic duct.
 d.h.' first hepatic duct.
 d.h.\" second „
 d.h-c. hepato-cystic duct.
 d.M. vestigial Müller's duct of the male.
 d.nas-lc. naso-lacrimal duct.
 d.p.d. dorsal pancreatic duct.

d.p.v. ventral pancreatic duct
d.pl. perilymphatic duct.
d.W. Wolffian duct.
duo. duodenum.

eb. parathyroid (epithelial body).
ep. epithelium.
epi. epiphysis.
ex.s.ly.sc." vessel from subscapular lymph sinus (pars dorsalis).
ex.s.ly.pect. vessel from pectoral lymph sinus.
ex.t.ly.l.sv. vessel from truncus lymphaticus longitudinalis subvertebralis.

fa.con. condylar facet.
fa.o.pr. facet for odontoid process of atlas.
fas.pl. fascia plantaris.
fbr.sh. fibrous sheath which surrounds the anus.

fen.b.nas. fenestra basalis nasi.
fen.bc.a. " basicranialis anterior.
fen.bc.p. " " posterior.
fen.d.nas. " dorsalis nasi.
fen.i.ch. " infra-conchalis.
fen.nar. " narina.
fen.ol. " olfactoria.
fo.ab. foramen abducens.
fo.au. " for the auditory nerve.
fo.el. " endolymphaticum.
fo.fac. " faciale.
fo.fac.' facial opening from the antrum petrosus laterale.
fo.i.den. inferior dental foramen.
fo.l.nas. foramen laterale nasi.
fo.m. " magnum.
fo.M. " of Monro.
fo.m.nas. " mediale nasi.
fo.men. mental foramina.
fo.n.sp. foramen for spinal nerve.
fo.n.sp.i " " first spinal nerve.
fo.n.sp.ii " " second " "
fo.n.5 " " trigeminus nerve.
fo.nt. " nutritium.
fo.o. " obturatorium.
fo.o-nas.l. " orbito-nasalis laterale.
fo.o-nas.m. " " " mediale.
fo.oc. " oculomotorium.
fo.op. " opticum.

fo.p.ot. foramen post-oticum.
fo.pal. foramen palatinum.
fo.per.c. " perforans carpi.
fo.per.t. " " tarsi.
fo.pl. " perilymphaticum.
fo.s.cor. " supracoracoideum.
fo.tr. " for the trochlear nerve.
fs.cu.v. fossa cubitalis ventralis.
fs.ol. olecranon fossa.
fs.tr. trochlear groove.
ft.b. fat body.
fv.c.fm. fovea capitis femoris.

g.coel. coeliac ganglion.
g.cop. ganglion copulare.
g.G. Gasserian ganglion.
g.il.a. anterior iliac ganglion.
g.il.p. posterior " "
g.pal. palatine ganglion.
g.scl.a. anterior subclavian ganglion.
g.scl.p. posterior " "
g.sp.io ganglion of the tenth spinal nerve.
g.7+8 ganglion acustico-faciale.
g.9+10 ganglion of the glossopharyngeus and vagus.
gl. glenoid cavity.
gl.b. gall-bladder.
gl.c. carotid labyrinth.
gl.cl.' cloacal gland, ventral portion.
gl.cl." " " dorsal "
gl.cut. dorsal venom glands.
gl.thy. thyroid gland.
gts. glottis.

h.ar. haemal arch.

Il. position of femoro-iliac joint.
in.cor. inscisa coracoidea.
inf. infundibulum.
int. intestine.

kd. kidney.

l.a. linea alba.
l.c.h. ligamentum coronarium hepatis.
l.d. dorsal mesentery.
l.h.c.p. ligamentum hepato-cavo-pulmonale.
l.h.e. ligamentum hepato-entericum.
l.il. ligament attaching femur to ilium.

l.ly.h. lateral lymph heart.
 l.mesc. mesocardial ligament.
 l.mch. mesorchium.
 l.ms. mesovarium.
 l.pb. ligament attaching femur to pubes.
 l.pl. pleural mesentery.
 l.t. ligamentum tubae.
 l.t.' " " , vestige in male.
 lag. lagena.
 lam.ter. lamina terminalis.
 liv. liver.
 lob.op. optic lobes.
 lu. lung.
 ly.s. lymph sinus.

m.a.d.5 musculus abductor digiti quinti.
 m.a.e.1 musculus abductor et extensor
 digiti primi.
 m.a.h.l. musculus anconaeus humeralis
 lateralis.
 m.a.h.m. musculus anconaeus humeralis
 medialis.
 m.a.s.m. musculus anconaeus scapularis
 medialis.
 m.ac.c. musculus anconaeus coracoideus.
 m.c. " cucullaris.
 m.c.' " " minor.
 m.c.b.l. " coraco-brachialis longus.
 m.c.d. musculi contrahentes digitorum.
 m.c.l. musculus constrictor laryngis.
 m.c.l.c. " caput longum muscu-
 lorum contrahentium.
 m.c.n. musculus constrictor naris.
 m.c.p.i.t. " caudali - pubo - ischio -
 tibialis.
 m.c.ph. musculus cephalo - dorso - sub-
 pharyngeus.
 m.c.r.' musculus coraco-radialis proprius,
 long tendon.
 m.cd.fm. musculus caudali-femoralis.
 m.d.h. " dorso-humeralis.
 m.d.l. " dilatator laryngis.
 m.d.m. " depressor mandibulae.
 m.d.n. " dilatator naris.
 m.d.n.' " " " ac-
 cessorius.
 m.d.s. musculus dorsalis scapulae.
 m.d.tr. " dorsalis trunci.
 m.de.d.4 musculus deductor digiti
 quarti.

m.e.a.c.r. musculus extensor antibrachii
 et carpi radialis.
 m.e.a.c.u. musculus extensor antebrachii
 et carpi ulnaris.
 m.e.b. musculi extensores breves digi-
 torum.
 m.e.c.r. musculus extensor carpi radialis.
 m.e.c.t. " " cruris tibialis.
 m.e.c.t.f. " " cruris et tarsi
 fibularis.
 m.e.c.u. musculus extensor carpi ulnaris.
 m.e.d. " " digitorum com-
 munis.
 m.e.i.l.t. musculus extensor iliobtibialis.
 m.e.i.l.t.' musculus extensor iliobtibialis,
 pars anterior.
 m.e.i.l.t." musculus extensor iliobtibialis,
 pars posterior.
 m.e.l.d.4 musculus extensor lateralis
 digiti quarti.
 m.e.t.t. musculus extensor tarsi tibialis.
 m.f.a.c.r. musculus flexor antibrachii et
 carpi radialis.
 m.f.a.c.u. musculus flexor antibrachii et
 carpi ulnaris.
 m.f.a.l. musculus flexor accessorius late-
 ralis.
 m.f.a.m. musculus flexor accessorius
 medialis.
 m.f.a.r. musculus flexor antebrachii radi-
 alis.
 m.f.b.p. musculi flexores breves pro-
 fundi.
 m.f.b.s. musculi flexores breves super-
 ficiales.
 m.f.c.r. musculus flexor carpi radialis.
 m.f.c.u. " " " ulnaris.
 m.f.f. " flexor fibularis.
 m.f.p. " primordialialis commu-
 nis.
 m.fm.f. musculus femoro-fibularis.
 m.g.hy. " geniohyoideus.
 m.g.gl. " genioglossus.
 m.h.a. musculus humero-antibrachialis.
 m.hy.gl. musculus hyoglossus.
 m.i.b. musculus interosseus antibrachii.
 m.i.c. " " cruris.
 m.i.c.i. musculus intertransversarius capi-
 tis inferior.
 m.i.hy. musculus interhyoideus.

m.i.hy.p. musculus interhyoideus posterior.	m.p.t. musculus pubo-tibialis.
m.i.m. " intermandibularis posterior.	m.pl." musculus plantaris superficialis minor (Eisler).
m.i.mc. musculi intermetacarpaceles.	m.r.a. musculus rectus anterior.
m.i.mt. " intermetatarsales.	m.r.ab. " " abdominis.
m.i.o. musculus obliquus inferior.	m.r.ab.' " " abdominis superficialis.
m.i.ph.3 " interphalangeus 3, &c.	m.r.ab." musculus rectus abdominis profundus.
m.i.s. " interspinalis.	m.r.c. musculus rectus cervicis.
m.il.cd. " ilio-caudalis.	m.r.c.' " " cervicis superficialis.
m.il.f. " ilio-fibularis.	m.r.c." musculus rectus cervicis profundus.
m.il.fm. " ilio-femoralis.	m.r.i. musculus rectus inferior.
m.is.cd. " ischio-caudalis.	m.r.p. " " posterior.
m.is.f. " ischio-flexorius, pars propria.	m.r.s. " " superior.
m.is.f.' musculus ischio-flexorius, pars plantaris.	m.rt.b. " retractor bulbi.
m.is.fm. musculus ischio-femoralis.	m.s. " subvertebralis.
m.l.a. musculus levator mandibulae anterior.	m.s.c. " supracoracoideus.
m.l.b. musculus levator bulbi.	m.s.hy. " subhyoideus.
m.l.b.p. musculus levator bulbi, pars principalis.	m.s.o. " obliquus superior.
m.l.b.s. musculus levator bulbi, pars sagittalis.	m.s.r.I " subarcualis rectus 1.
m.l.b.s.' musculus levator bulbi, pars sagittalis, caput laterale.	m.s.s. " subcoraco-scapularis.
m.l.b.s." musculus levator bulbi, pars sagittalis, caput mediale.	m.t. " transversalis.
m.l.b.t. musculus levator bulbi, pars transversalis.	m.t.s. " thoraci-scapularis.
m.l.e. musculus levator mandibulae externus.	m.t.v.4 " transversus ventralis 4.
m.l.p. musculus levator mandibulae posterior.	m.y.p. " ypsiloideus posterior.
m.o. musculus opercularis.	mand. lower jaw.
m.o.e.' musculus obliquus externus superficialis.	me.i.c. membrana intercartilaginea.
m.o.i. musculus obliquus inferior.	med.ob. medulla oblongata.
m.o.int. musculus obliquus internus.	mem.iv. membrane closing the intervertebral foramen.
m.o.s. musculus obliquus superior.	mes. mesentery.
m.p. musculus pectoralis.	musc. muscle.
m.p.fm. musculus pubi-femoralis.	myo. myoseptum.
m.p-h. musculus procoraco-humeralis.	n.acc. nervus vagi, ramus accessorius.
m.p.i.f.e. musculus pubo-ischio-femoralis externus.	n.ax. " axillaris.
m.p.i.f.i. musculus pubo-ischio-femoralis internus.	n.br. " brachialis.
m.p.i.t. musculus pubo-ischio-tibialis.	n.c.a. " cardiacus anterior.
m.p.p. " pronator profundus.	n.c.fm.l. nervus cutaneus femoris lateralis.
m.p.s. " pectori-scapularis.	n.c.fm.m. nervus cutaneus femoris medialis.
	n.c.fm.p. nervus cutaneus femoris posterior.
	n.c.fm.v. nervus cutaneus femoris ventralis.
	n.c.p. nervus cardiacus posterior.

- n.sp.3 third spinal nerve.
 n.sp.4 fourth " "
 n.sp.5 fifth " "
 n.sp.15 fifteenth " "
 n.sp.16 sixteenth " "
 n.sp.17 seventeenth spinal nerve.
 n.sp.18 eighteenth " "
 n.tr.int.acc. truncus intestino-accessorius
 n. vagi.
 n.ul. nervus ulnaris.
 n.ul.r.m. nervus ulnaris, ramus medianus.
 n.vis.a. anterior visceral nerve (sympa-
 thetic).
 n.vis.m. middle visceral nerve (sympa-
 thetic).
 n.vis.4 nerve of the fourth visceral arch.
 n.vis.5 " " fifth " "
 n.1 nervus olfactorius.
 n.1.d. nervus olfactorius, dorsal branch.
 n.1.v. " " ventral branch.
 n.2 nervus opticus.
 n.3 " oculomotorius.
 n.3.i. " oculomotorius, ramus in-
 ferior.
 n.3.s. nervus oculomotorius, ramus su-
 perior.
 n.3-5 ramus communicans n.3 ad 5.
 n.4 nervus trochlearis (or patheticus).
 n.4a nervus trochlearis, anastomosing
 branch.
 n.4b nervus trochlearis, direct branch.
 n.5 nervus trigeminus.
 n.5a nervus trigeminus, ramus ophthal-
 micus profundus.
 n.5a.L. lateral terminal branch of r.
 ophthal. prof.
 n.5a.M. mesial terminal branch of r.
 ophthal. prof.
 n.5a.V. ventral terminal branch of r.
 ophthal. prof.
 n.5b nervus trigeminus, ramus maxil-
 laris.
 n.5c nervus trigeminus, ramus man-
 dibularis.
 n.6 nervus abducentis.
 n.7 " facialis.
 n.7+8 acustico-facialis root.
 n.8.a nervus auditorius, anterior ramus.
 n.8.m. " " mesial ramus.
 n.8.p. " " posterior ramus.
 n.9 nervus glossopharyngeus.
 n.9+10 glossopharyngeus-vagus root.
 n.10 nervus vagus.
 n.a nerve to skin of lateral surface of
 arm.
 n. β nerve to skin over the procoracoid.
 n. γ " " " scapula.
 na.cap. nasal capsule.
 nar.e. external nares.
 nar.i. internal nares.
 nl.sp. neural spine.
 nod.ch. nodus chorioideus.
 o.art. articular ossification in Meckel's
 cartilage.
 o.c. os centrale.
 o.b.c.1+2 fused basal carpals of the 1st
 and 2nd fingers.
 o.b.c.4 basal carpal for the fourth finger.
 o.b.t.1+2 fused basal tarsals of the 1st
 and 2nd toes.
 o.b.t.4 basal tarsal of the fourth toe.
 o.b.t.5 " " " fifth toe.
 o.den. dentary.
 o.f. fibula.
 o.fb. fibulare.
 o.fm. femur.
 o.fr. frontal.
 o.h. humerus.
 o.i. intermedium.
 o.il. ilium.
 o.is. ischium.
 o.m. maxilla.
 o.m-M. mento-Meckelian.
 o.mc.1 metacarpal of the first finger.
 o.mc.4 " " fourth "
 o.mt.1 metatarsal of the first toe.
 o.mt.2 " " second toe.
 o.mt.4 " " fourth toe.
 o.mt.5 " " fifth toe.
 o.nas. nasal.
 o.o-s. orbito-sphenoid.
 o.oc-pt. occipito-petrosal.
 o.p-art. pre-articular.
 o.p-fr. pre-frontal.
 o.p-m. pre-maxilla.
 o.p-v. pre-vomer.
 o.par. parietal.
 o.pb-is. pubo-ischium.
 o.ps. parasphenoid.

o.pt. pterygoid (osseous).
 o.qu. quadratæ.
 o.r. radius.
 o.sc. scapula.
 o.sq. squamosal.
 o.t. os triangulare.
 o.tb. tibia.
 o.u. ulna.
 o.u.+i.' fused ulnare and intermedium,
 pars intermedia.
 o.u.'+i. fused ulnare and intermedium,
 pars ulnaris.
 od. oviduct.
 oes. oesophagus.
 op.ch. optic chiasma.
 ost.od.e. external opening of the oviduct.
 ost.od.i. internal opening of the oviduct.
 ov. ovary.
 p.card. pericardium.
 p.o.n. peri-orbital network.
 p.bas. pars basilaris.
 p.neg. pars neglecta.
 pan. pancreas.
 pap.cl. cloacal papilla.
 pap.u-g. urino-genital papilla.
 par. paraphysis.
 per. line of attachment of pericardium to
 heart.
 pit. pituitary body.
 pit.' " " pars intermedia.
 pit." " " " anterior.
 pit.'" " " " tuberalis.
 pl.ch.ven.1 chorioid plexus of the first
 ventricle.
 pl.ch.ven.4 chorioid plexus of the fourth
 ventricle.
 pl.l. lateral plexus (covering the saccus
 endolymphaticus).
 pl.ph. pharyngeal plexus.
 plc.hy.m. plica hyomandibularis.
 pr.asc. processus ascendens.
 pr.ba. " basalis.
 pr.cor. coronoid process.
 pr.nas. processus prenasalis.
 pr.o. odontoid process.
 pr.ol. olecranon "
 pr.ot. processus oticus.
 pr.p-p. pre-pubic process.
 pr.S. 'Gaumenfortsatz' of Seydel.

pr.tch. trochanter.
 pr.tr. transverse process.
 py. pylorus.
 r.al. ramus alveolaris VII.
 r.com.ad.sym. ramus communicans to
 the sympathetic.
 r.com.1-2 ramus communicans from
 the second to the first spinal nerve.
 r.com.2-3 ramus from the second to
 the third spinal nerve.
 r.9+10-7 ramus communicans from
 cranial nerves IX and X to VII.
 rb. rib.
 rb.2 rib of second vertebra.
 rb.3. " third "
 rec.pr-op. recessus pre-opticus.
 rec.sem. receptaculum seminis.
 rec.utric. recessus utriculi.
 rect. rectum.
 s.ly.anas. sinus lymphaticus anastomoticus.
 s.ly.br. " " branchialis.
 s.ly.cl. cloacal lymph sinus.
 s.ly.f. lymph sinus from post-axial side of
 hind-limb.
 s.ly.hy. hyoidean lymph sinus.
 s.ly.hyp. hypoglossal lymph sinus.
 s.ly.il. iliac " "
 s.ly.ing. inguinal " "
 s.ly.j. jugular " "
 s.ly.m. median " "
 s.ly.m.pf. deep mandibular lymph sinus.
 s.ly.man. mandibular lymph sinus.
 s.ly.p-o. peri-orbital " "
 s.ly.pan. peri-anal " "
 s.ly.pect. pectoral " "
 s.ly.pel. pelvic " "
 s.ly.r. lymph sinus from pre-axial side of
 fore-limb.
 s.ly.ren. renal lymph sinus.
 s.ly.sc.' subscapular lymph sinus, pars
 ventralis.
 s.ly.sc." subscapular lymph sinus, pars
 dorsalis.
 s.ly.t. lymph sinus from pre-axial side of
 hind-limb.
 s.ly.th. thyroidean lymph sinus.
 s.ly.u. lymph sinus from post-axial side of
 fore-limb.

s.ly.ves. vesicular lymph sinus.
s.s.utric. sinus superior utriculi.
s.sag. „ sagittalis.
s.v. „ venosus.
sac. sacculus.
sac.cop. saccus copularis.
sc. position of humero-scapular joint.
sep.a-p. septum aortico-pulmonale.
sep.ac. „ accessorium.
sep.c. „ caroticum.
sep.c-a. „ carotico-aorticum.
sep.p. „ pulmonale.
sep.tr. „ transversum.
sp. spleen.
stom. stomach.
su.l.d. sulcus longitudinalis dorsalis.
su.l.v. „ „ ventralis.
sym.d. dorsal sympathetic chain.
sym.v. ventral „ „

t.a. truncus arteriosus.
t.ly.cd. truncus lymphaticus caudalis.
t.ly.circ.sc. truncus lymphaticus circum-
flexus scapulae.
t.ly.il. truncus lymphaticus iliacus.
t.ly.l.l. truncus lymphaticus longitudi-
nalis lateralis.
t.ly.l.pab. truncus lymphaticus longitu-
dinalis parabdrominalis.
t.ly.l.pe. truncus lymphaticus longitudi-
nalis parepigastricus.
t.ly.l.sv. truncus lymphaticus longitudi-
nalis subvertebralis.
t.ly.p-ph. truncus lymphaticus peripha-
ryngeus.
t.ly.pud. truncus lymphaticus pudendus.
tes. testis.
thc. thalamencephalon.
tr.ch. tracheal chamber.

utr. ureters.

v.abd. vena abdominalis.
v.anas. „ anastomotica.
v.anas.br. vena anastomotica brachii.
v.ax. vena axillaris.
v.br.l. „ brachialis lateralis.
v.br.m. „ „ medialis.
v.c.p. „ cava posterior.
v.card.p. vena cardinalis posterior.

v.cd. vena caudalis.
v.circ.sc. „ circumflexa scapulae.
v.cl.l. „ cloacae lateralis.
v.cl.m. „ cloacae medialis.
v.col.fem. „ collateralis femoris.
v.cr.m-ot. „ cranialis mesotica.
v.cr.ob. „ „ obliqua.
v.cr.po-ot. „ „ post-otica.
v.cr.pr-ot. „ „ pro-otica.
v.cut.d.sc.a. vena cutanea dorsalis sca-
pulae anterior.
v.cut.d.sc.p. vena cutanea dorsalis sca-
pulae posterior.
v.cut.fem.p.l. vena cutanea femoris pos-
terior lateralis.
v.cut.pa. vena cutanea parva.
v.d.sc. vena dorsalis scapulae.
v.e.a. „ epigastrica anterior.
v.e.m. „ „ medialis.
v.f.c. „ facialis communis.
v.f.i. „ „ inferior.
v.f.s. „ „ superior.
v.fr. „ frontalis.
v.g.lien. „ gastrico-lienalis.
v.gen.s. „ genitalis (left).
v.h.s. „ hepatica (left).
v.hm. „ haemorrhoidalis.
v.il.com. „ iliaca communis.
v.il.tr. „ iliaca transversa.
v.in.p. „ intestinalis posterior.
v.is. „ ischiadica.
v.J. „ Jacobsoni.
v.j.e. „ jugularis externa.
v.j.i. „ „ interna.
v.j.l. „ „ lateralis.
v.l. „ lateralis.
v.ling. „ lingualis.
v.long.di. „ longitudinalis diencephali.
v.m.i. „ mandibularis interna.
v.m.pf. „ „ profunda.
v.max.pal. „ maxillo-palatina.
v.na. „ nasalis.
v.o.i. „ orbitalis inferior.
v.o.na. „ orbito-nasalis.
v.o.s. „ orbitalis superior.
v.od.a. „ oviducalis anterior.
v.od.long. „ „ longitudinalis.
v.od.p. „ „ posterior.
v.op. „ ophthalmica.
v.p. „ porta.

v.p.mi.	vena porta minor.	v.v.	vena vertebralis.
v.pal.	„ palatina.	v.v.rect.	„ ventralis recti.
v.pal.l.	„ „ lateralis.	v.ves.a.	„ vesicalis anterior.
v.palp.i.	„ palpebralis inferior.	v.ves.d.	„ „ dorsalis.
v.palp.s.	„ „ superior.	v.ves.hm.	„ vesico-haemorrhoidalis.
v.par.l.	„ parietalis lateralis.	v.ves.p.	„ vesicalis posterior.
v.pect.	„ pectoralis.	va.eff.	vasa efferentia.
v.pel.	„ pelvica.	ven.	ventricle.
v.pet.l.	„ petrosa lateralis.		
v.ph-p.	„ pharyngo-palatina.	x.	anomalous pharyngeal branch of a.pet.l.
v.pit.	„ pituitaria.		
v.po-oc.	„ post-occipitalis.	zy.a.	anterior zygapophysis.
v.pt.	„ pterygoidea.	zy.p.	posterior „
v.pud.	„ pudenda.		
v.pul.	„ pulmonalis.	†	points at which femur is attached by the cotyloid ligament.
v.pul.s.	„ „ (left).	‡	point of junction between 'oviducal' and 'uterine' portions of the oviduct.
v.R.	„ Rusconii.		
v.scl.	„ subclavia.		
v.sup.cor.	„ supracoracoidea.		
v.th.	„ thyroidea.		

EXPLANATION OF PLATES

All magnifications are to be regarded as approximate

PLATE I

- Fig. 1. *Skull*, dorsal view, $\times 5$. The investing bones have been removed from the right side so as to reveal the primary cranium. In this and in all subsequent figures of the skeleton the persisting cartilage is dotted.
- Fig. 2. *Skull*, ventral view, $\times 5$. The investing bones have been removed from the right-hand side (left side of figure).

PLATE II

- Fig. 3. *Skull*, lateral view, $\times 5$.
- Fig. 4. *Skull* seen in sagittal section showing the interior of the *cavum cranii*, $\times 5$.
- Fig. 5. *Skull*, occipital view, $\times 5$.
- Fig. 6. *Hyobranchial apparatus* viewed from the dorsal side, $\times 5$. The cerato-hyals are shown laterally displaced for sake of clearness. Normally their anterior ends overlap one another and lie ventral to the hypo-hyals.
- Fig. 7. *Lower Jaw*, mesial aspect, $\times 5$. Left side only shown.

PLATE III

- Fig. 8. *Lower Jaw*, lateral aspect, $\times 5$. Right side only shown.
- Fig. 9. *Lower Jaw*, dorsal aspect, $\times 5$. Right side only shown.
- Fig. 10. '*Atlas*' *Vertebra*, seen from the side, $\times 5$.
- Fig. 11. '*Atlas*' *Vertebra*, anterior view, $\times 5$.
- Fig. 12. *Second and Third Vertebrae*, seen from the side, $\times 5$.
- Fig. 13. *Last Pre-sacral Vertebra*, dorsal view, $\times 5$.
- Fig. 14. *Last Pre-sacral Vertebra*, ventral view, $\times 5$.
- Fig. 15. *Last Pre-sacral Vertebra*, seen from the side, $\times 5$.
- Fig. 16. *Last Pre-sacral Vertebra*, anterior view, $\times 5$.
- Fig. 17. *Last Pre-sacral Vertebra*, posterior view, $\times 5$.
- Fig. 18. *Fourth Caudal Vertebra*, seen from the side, $\times 5$.
- Fig. 19. *Fourth Caudal Vertebra*, ventral view, $\times 5$.

PLATE IV

- Fig. 20. *Right Half of the Pectoral Girdle*, viewed from the ventro-lateral aspect, $\times 5$.
- Fig. 21. *Right Half of the Pectoral Girdle*, viewed from the mesio-dorsal aspect, $\times 5$.
- Fig. 22. *Sternum*, viewed from the ventral side, $\times 5$.
- Fig. 23. *Right Humerus*, viewed from the extensor side, $\times 5$.
- Fig. 24. *Right Humerus*, viewed from the flexor side, $\times 5$.
- Fig. 25. *Right Ulna*, viewed from the extensor side, $\times 5$.
- Fig. 26. *Right Ulna*, viewed from the post-axial side, $\times 5$.
- Fig. 27. *Right Ulna*, viewed from the flexor side, $\times 5$.
- Fig. 28. *Left Fore-arm and Carpus*, viewed from the extensor (dorsal) side. The radius and ulna are somewhat fore-shortened, $\times 5$.

PLATE V

- Fig. 29. *Right Leg and Tarsus*, viewed from the extensor aspect, $\times 5$.
- Fig. 30. *Left Leg and Tarsus*, viewed from the flexor aspect, $\times 5$.

- Fig. 31. *Right Femur*, viewed from the pre-axial side, $\times 5$.
 Fig. 32. *Right Femur*, viewed from the extensor side, $\times 5$.
 Fig. 33. *Right Femur*, viewed from the flexor side, $\times 5$.
 Fig. 34. *Right Half of the Pelvic Girdle*, viewed from the ventro-lateral side, $\times 5$.
 Fig. 35. *Right Half of the Pelvic Girdle*, viewed from the mesio-dorsal side, $\times 5$.
 Fig. 36. *Ypsiloid Cartilage*, ventral aspect, $\times 5$.

PLATE VI

- Fig. 37. *Dissection of the Ventral Side of the Head*. On the left side of the figure the skin only has been removed, while on the right the superficial muscles (MM. intermandibularis and interhyoideus) have also been cut away to show the deeper structures, $\times 4$.
 Fig. 38. *Dissection of the Ventral Side of the Head*. On the left side of the figure all but the deepest muscles have been removed, thus exposing the hyobranchial skeleton, while on the right side this skeleton has also been taken away to show the structures on the mouth floor, $\times 4$.

PLATE VII

- Fig. 39. *Right Radius*, viewed from the extensor side, $\times 5$.
 Fig. 40. *Right Radius*, viewed from the pre-axial side, $\times 5$.
 Fig. 41. *Right Radius*, viewed from the flexor side, $\times 5$.
 Fig. 42. *Right Humerus*, viewed from the post-axial side, $\times 5$.
 Fig. 43. *Superficial Extensor Muscles of the Shoulder and Fore-limb*. Viewed from the dorso-lateral aspect, $\times 4$.
 Fig. 44. *Deeper Extensor Muscles of the Right Fore-arm and Hand*, as revealed by removing the M. extensor digitorum communis, $\times 4$.
 Fig. 45. *Superficial Flexor Muscles of the Pectoral Region and Left Fore-limb*, $\times 4$.
 Fig. 46. *Deeper Flexor Muscles of the Left Fore-arm and Hand*, as revealed by removing the M. flexor primordialis communis. The third and deepest layer of flexor muscles cannot be seen, $\times 4$.

PLATE VIII

- Fig. 47. *Superficial Extensor Muscles of the Right Hind-limb*, $\times 4$.
 Fig. 48. *Superficial Flexor Muscles of the Right Hind-limb*, $\times 4$.
 Fig. 49. *Deeper Flexor Muscles of the Right Hind-limb*, the third and deepest stratum of flexor muscles is not visible, $\times 4$.

PLATE IX

- Fig. 50. *Sagittal Section of the Brain*. The plexuses are diagrammatic, $\times 8$.
 Fig. 51. *Brain*, dorsal view. The main veins and venous plexuses are also shown on the left, $\times 8$.
 Fig. 52. *Brain*, ventral view. The main cerebral arteries are also shown, $\times 8$.
 Fig. 53. *M. levator bulbi seen from above*, semi-diagrammatic after Luther.

PLATE X

- Fig. 54. *Semi-diagrammatic Representation of the Cranial Nerves*. The nerves which normally lie on the ventral side of the mouth and pharynx are shown turned out to the left. This has resulted in a somewhat disproportioned elongation of the tenth cranial and first spinal nerves. The relation of the nerves to the arterial arches is also shown. The positions of the sense capsules are indicated by dotted lines.

PLATE XI

- Fig. 55. *Brachial Plexus, and Nerves of the Fore-limb*, semi-diagrammatic. The nerves are those of a right limb seen from the ventral side. Distal to the shoulder, the extensor nerves are black and the flexor nerves clear. The position of the humero-scapular joint is shown.

PLATE XII

- Fig. 56. *Sciatic Plexus and Nerves of the Hind-limb*, semi-diagrammatic. The treatment has been the same as in the previous figure.

PLATE XIII

- Fig. 57. *Nerves of the Orbit and the Eye Muscles*, shown semi-diagrammatically. The M. retractor bulbi and M. rectus posterior have been turned back. Normally the former muscle would encircle the optic nerve. The oculomotor nerve is black, while the other nerves have been left clear. The positions of the orbital margins, the nasal capsule, and the internal naris have been indicated in outline.
- Fig. 58. *Blood-vessels of the Orbit*, somewhat schematized. The arteries are striped and the veins have been left clear. The position of the antrum petrosum laterale lies between the processes of the palato-pterygoid. The limits of the orbit are shown in outline.
- Fig. 59. *Heart*, seen from the dorsal side. The pericardial attachment is indicated by a heavy dotted line, $\times 4$.
- Fig. 60. *Heart*, seen from the ventral side. The pericardial attachment indicated as above, $\times 4$.

PLATE XIV

- Fig. 61. *Scheme of the Arterial System* viewed from the ventral side. The most dorsal vessels are black, the most ventral have been left clear, and the intermediate ones have their relative depth indicated by the intensity of the striping. The positions of the limb axes are indicated thus, \oplus .

PLATE XV

- Fig. 62. *Scheme of the Venous System*, viewed from the ventral side. In general the deeper vessels are shown on the left of the figure. The limb axes are indicated as above.

PLATE XVI

- Fig. 63. *Dissection of the Pelvis* from the ventral side showing the Renal-portal System of veins and the related Arteries. On the left side of the figure the pelvic girdle is shown cut through its symphysis and turned back, and on this side also a semi-diagrammatic transverse section of the thigh is shown. On the right of the figure the head of the femur and the whole of the pelvic girdle, with the exception of a small portion of the ilium, have been removed, while the muscles on this side are incompletely drawn to allow room for the lettering. The trunk muscles anteriorly and the caudal muscles posteriorly are shown in semi-diagrammatic transverse section.

PLATE XVII

- Fig. 64. *Dorsal Aorta* carefully drawn from a single female specimen, together with the *post-cardinal veins* and the *cervical and abdominal portions of the sympathetic nervous system*, $\times 2\frac{1}{2}$.

Fig. 64a. *Suprarenal and Median Cloacal Arteries of the Male*, $\times 2\frac{1}{2}$.

Fig. 65. Reconstruction in the solid of the *Lateral Vein, Lateral Lymphatic Trunk*, and *Lateral Lymph Hearts*, seen from the ventral side, after Hoyer and Udziela.

Fig. 66. Ditto, seen from the dorsal side.

Fig. 67. *Horizontal Longitudinal Section of the Lateral Vein and Lymphatic Trunk* showing the *Lateral Lymph Hearts*. Modified after Hoyer and Udziela, and representing the larval condition.

PLATE XVIII

Fig. 68. *Lymphatics of the Pectoral Region and of the Floor of the Mouth*, ventral view. On the left side of the figure the subscapular, the thyroid, and the hypoglossal lymph sinuses have been removed and the deeper sinuses exposed. Somewhat schematized. Subcutaneous network not shown.

Fig. 69. *Lymphatics of the Pelvis*. On the left of the figure the skin and subcutaneous network only have been removed, and on the right the superficial sinuses and the pelvic girdle, as well as a portion of the vesicular sinus, have been cut away so as to expose the deeper sinuses. Somewhat schematized.

PLATE XIX

Fig. 70. *Blood-vessels and Lymphatics of the Palate*, seen from the ventral side. The blood-vessels are shown on the right of the figure and the lymphatics on the left. The arteries are striped, the veins left clear, and the lymphatics are black.

Fig. 71. *Transverse Section through the Anterior End of the Cloaca of the Male* showing the urino-genital papillae and the opening of the bladder. Schematized, $\times 9$.

PLATE XX

Fig. 72. *Female Urino-genital System*, seen from the ventral side. The left ovary and the posterior portion of the right oviduct have been removed. The cloaca has been split open mid-ventrally, and the left lung has also been removed.

PLATE XXI

Fig. 73. *Male Urino-genital System*, ventral view. On the left of the figure the lung and a portion of the mesorchium have been removed, and the Wolffian duct cut through at its entrance into the cloaca and turned over to display the ureters. On the right the lung, fat-body, testes, Wolffian duct, and ureters are in their normal positions, but the ventral portion of the cloacal gland has been removed.

Fig. 74. *Diagrammatic Representation of the Male Urino-genital system* to show the course of the sperms through the kidney and Wolffian duct to the exterior. Vasa efferentia black, Wolffian duct and its tributaries striped, and the ureters dotted.

PLATE XXII

Fig. 75. *Alimentary Canal and its Associated Glands and the Hepatic Portal System*, seen from the ventral side. The mesentery has been cut to allow the intestine to be displayed, and the cut edges are indicated by a double dotted line. The liver is turned over to the right (left as viewed). (The plica gastro-lienalis and p. recto-lienalis not shown.)

Fig. 76. *Dissection of the Gall-bladder and Bile-ducts* seen from the ventral side. A portion of the right lobe of the liver and the head of the ventral pancreas have been removed in order to display the ducts.

PLATE XXIII

- Fig. 77. *Respiratory Organs, Larynx, Tracheal Chamber, and Lungs*, seen from the ventral side. The tracheal chamber on the right of the figure shows the *Glottis*, the *Laryngeal Cartilages*, and the *Entrance to the Lung*. The *M. transversus ventralis* 4 has been removed from the left side of the figure as also have the pulmonary vein and the anterior pulmonary nerve, $\times 6$.
- Fig. 78. *Dorsal View of Two Vertebrae with Two of the Dorsal Myosepta attached on the Left Side*. The *MM. interspinales* are also shown, $\times 5$.

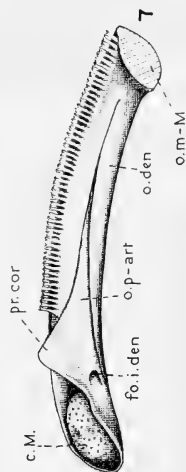
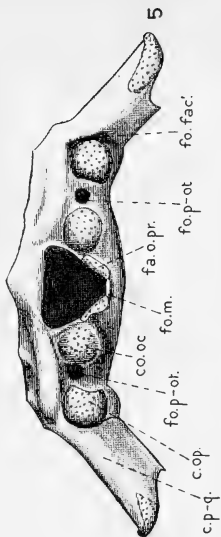
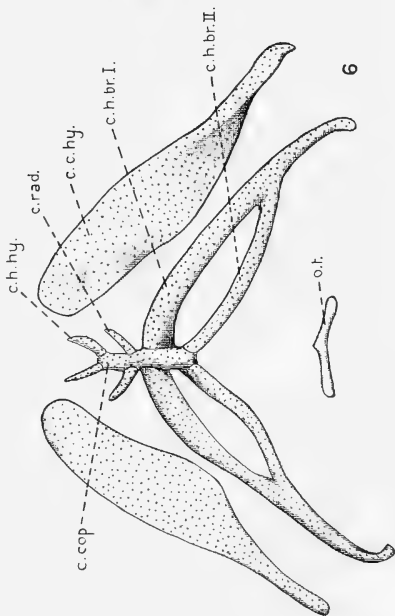
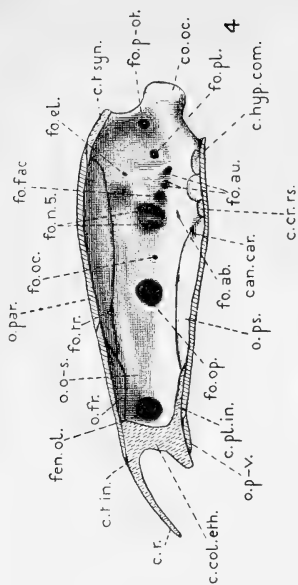
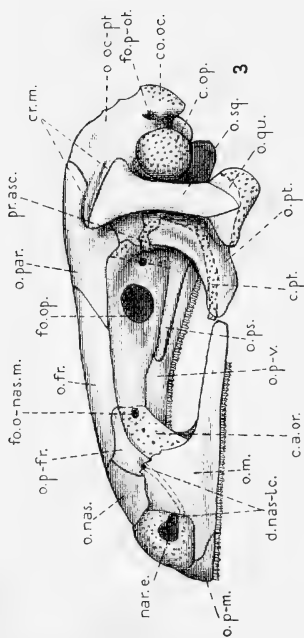
PLATE XXIV

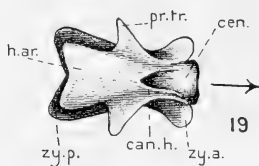
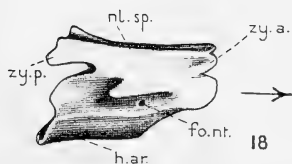
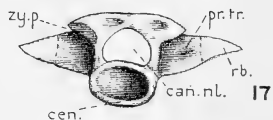
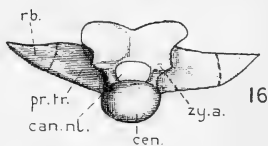
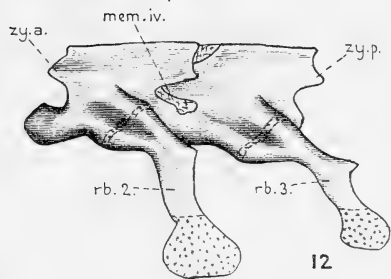
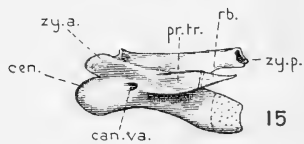
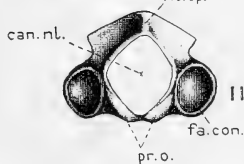
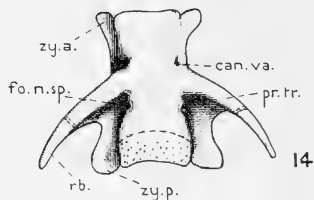
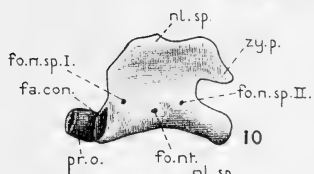
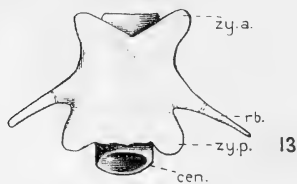
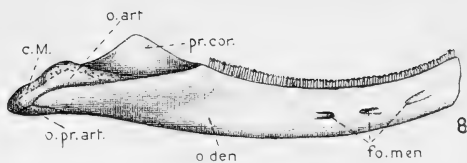
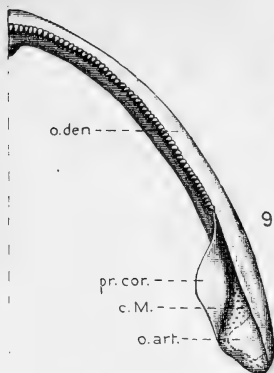
- Fig. 79. Semi-diagrammatic representation of the *Tenth Spinal Nerve* illustrating the typical branches of an abdominal nerve.
- Fig. 80. *Membranous Labyrinth of the Ear*, viewed from the lateral aspect, $\times 25$.
- Fig. 81. *Membranous Labyrinth of the Ear*, viewed from the mesial aspect, $\times 25$.
- Fig. 82. *Lateral View of the Cartilaginous Nasal Capsule* with the smooth nasal muscles in situ. Modified after Bruner.

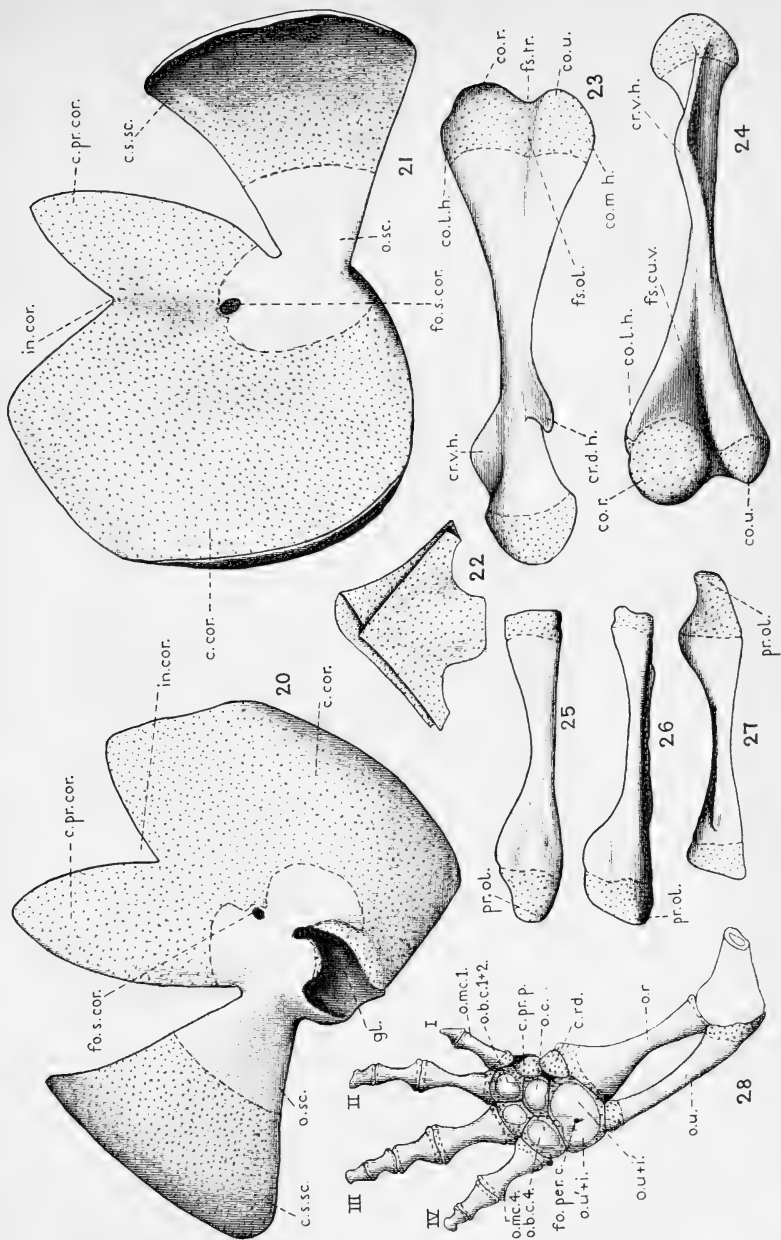
PLATE XXV

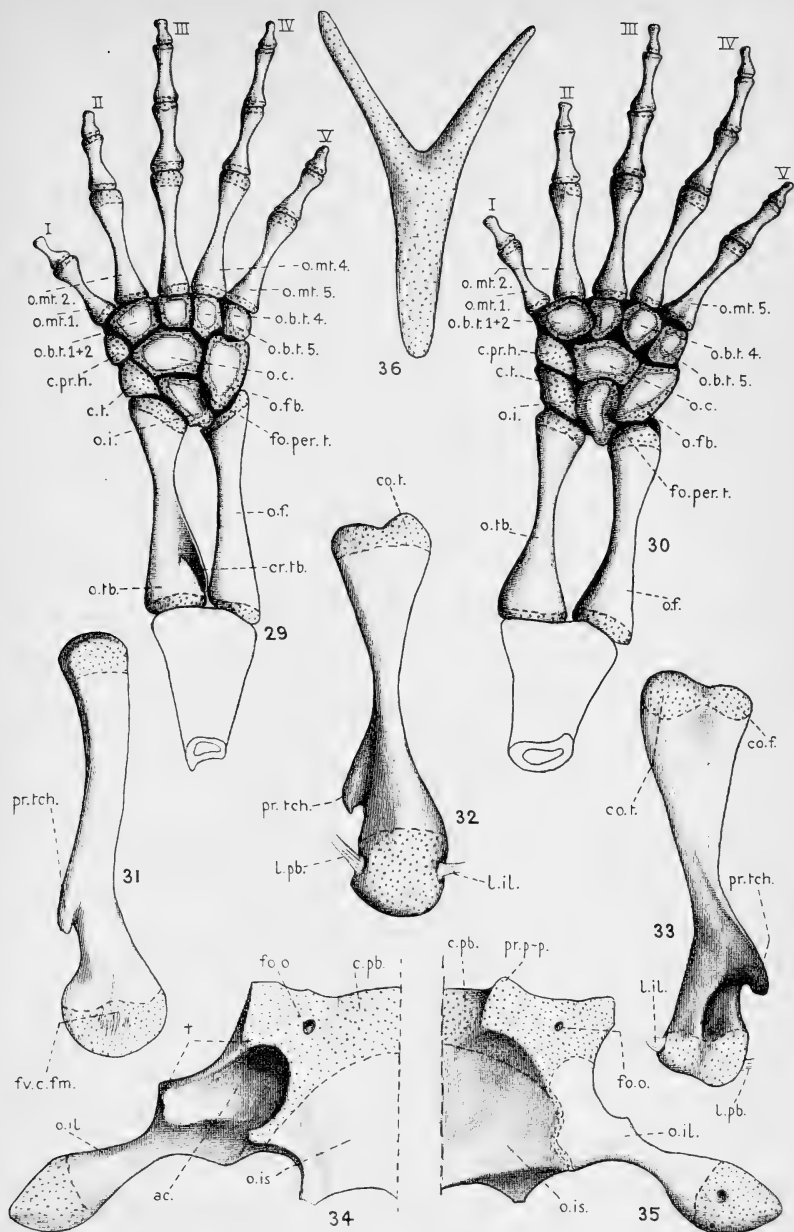
- Fig. 83. Map of Europe—including Asia Minor—showing the distribution of the *Genus Salamandra*. The area covered by *S. semenovi* is somewhat speculative since the records are very scanty.
- Fig. 84. Map of Europe showing the distribution of the three major varieties of the species of *S. salamandra*. *Note*: the ordinary *Forma typica* is also found all over the area covered by *var. mollerii*.

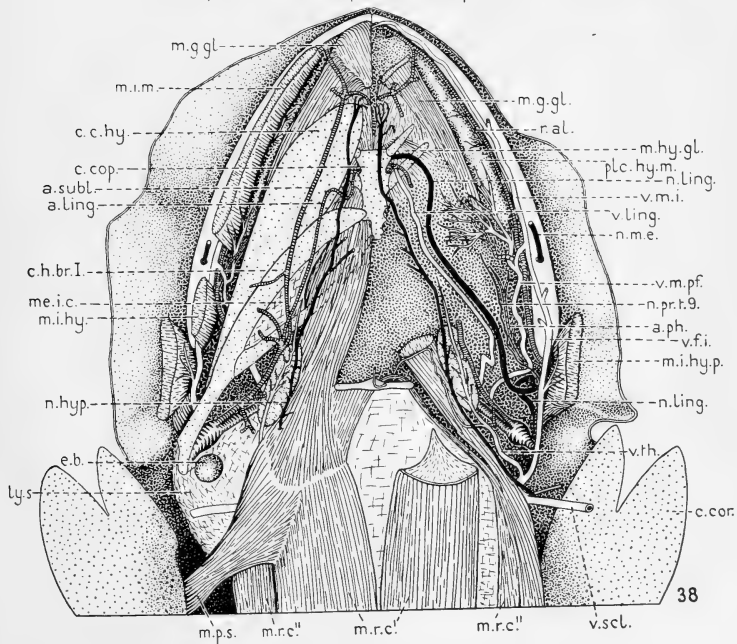
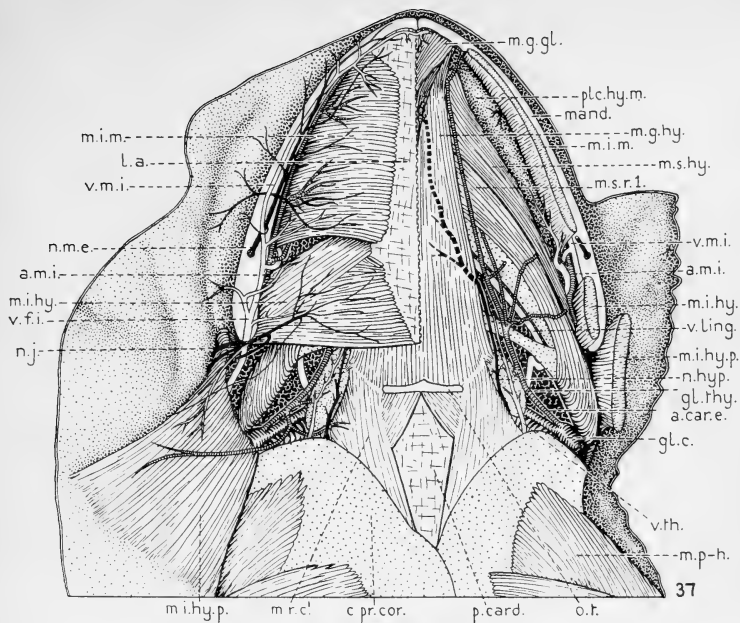
PLATES

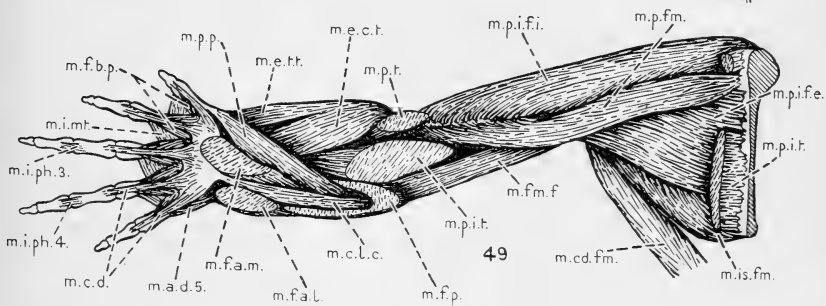
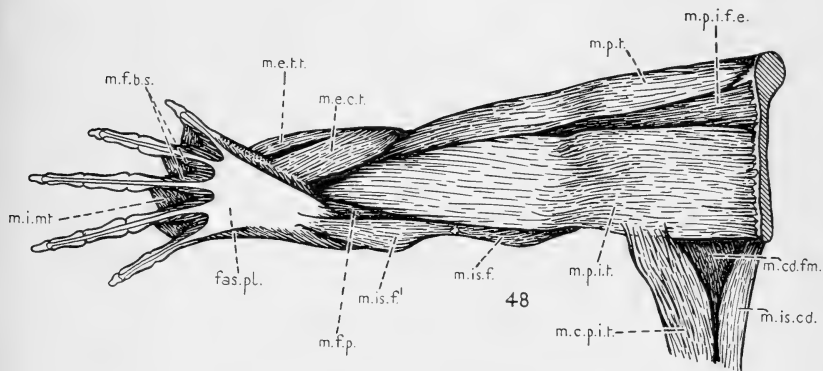
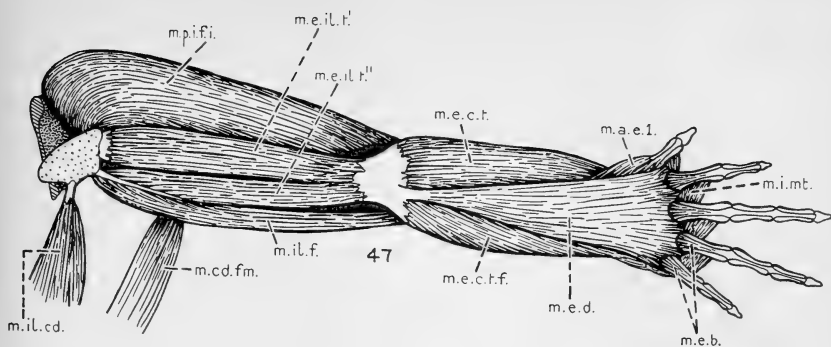


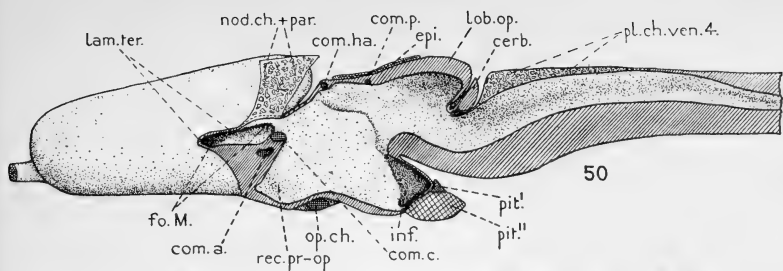




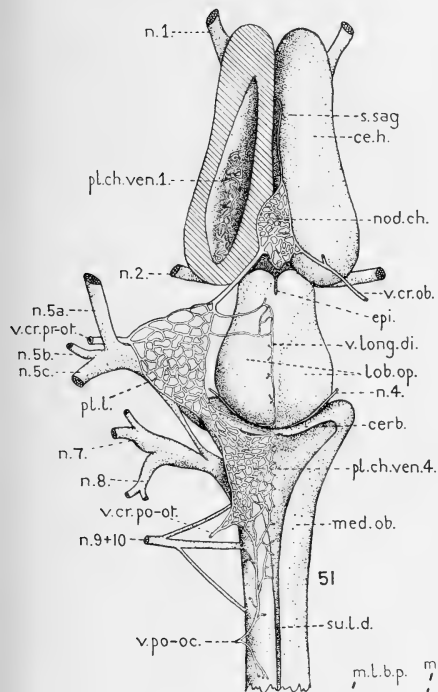




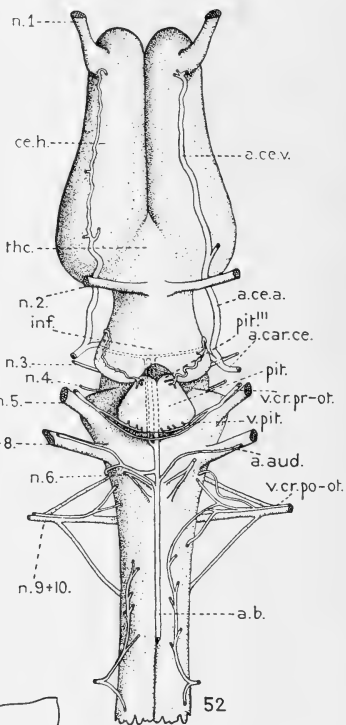




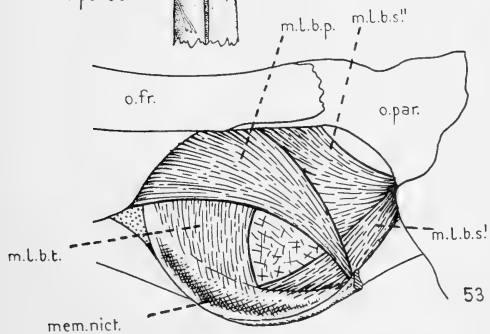
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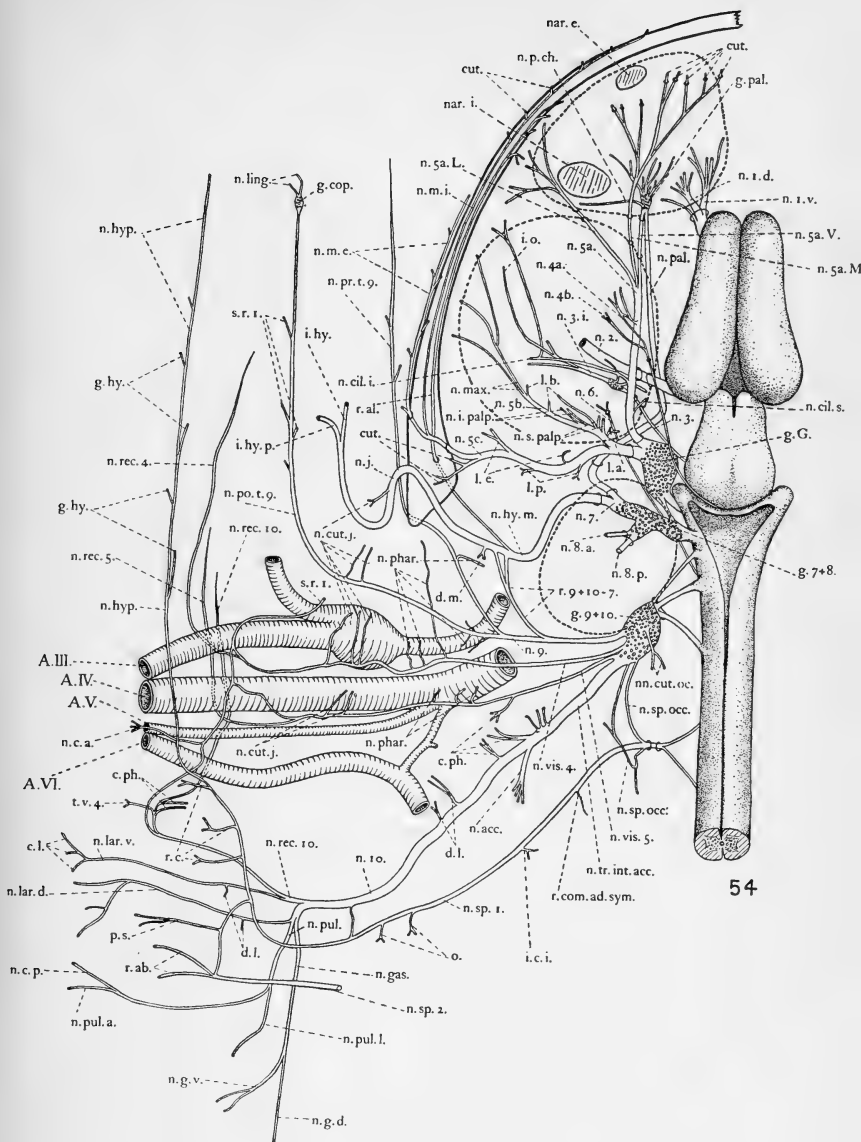
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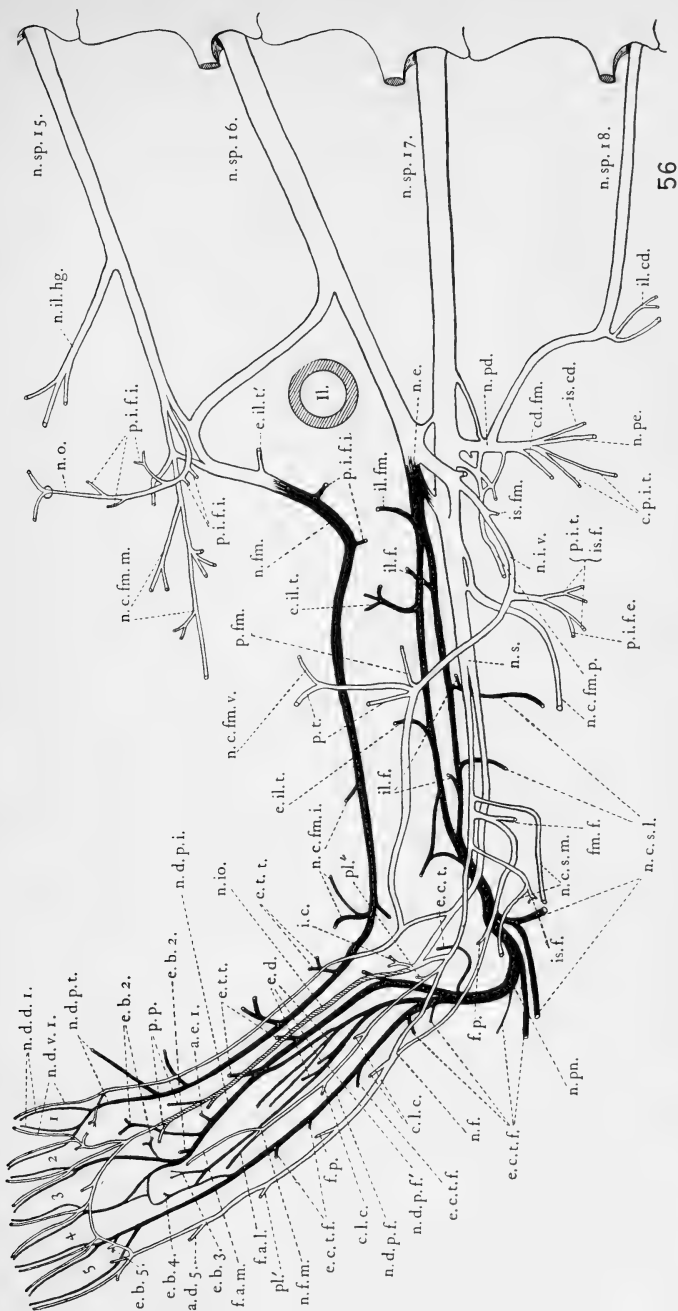


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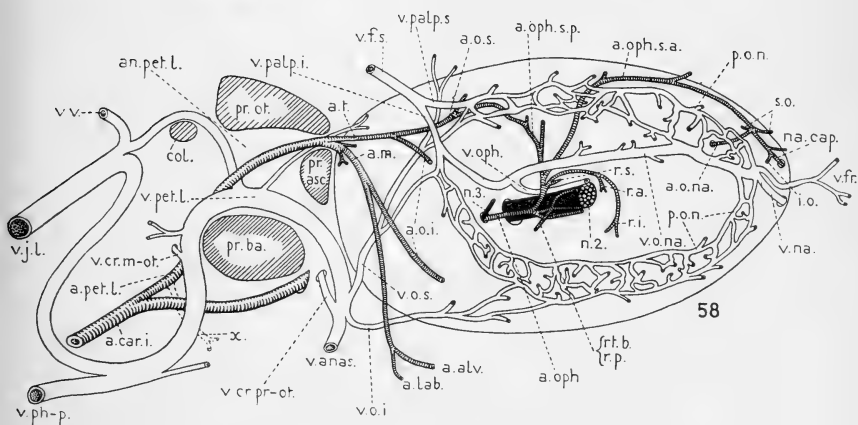
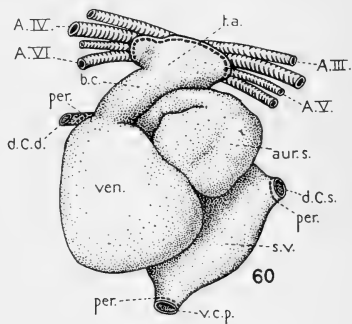
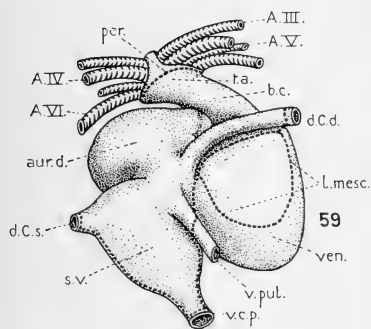
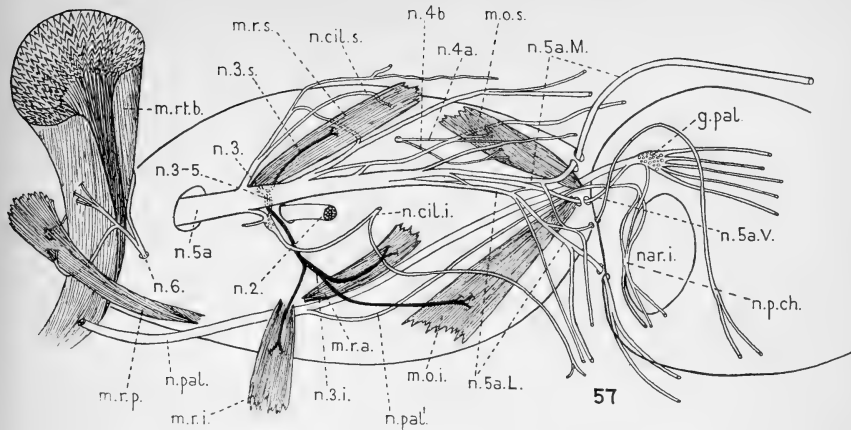


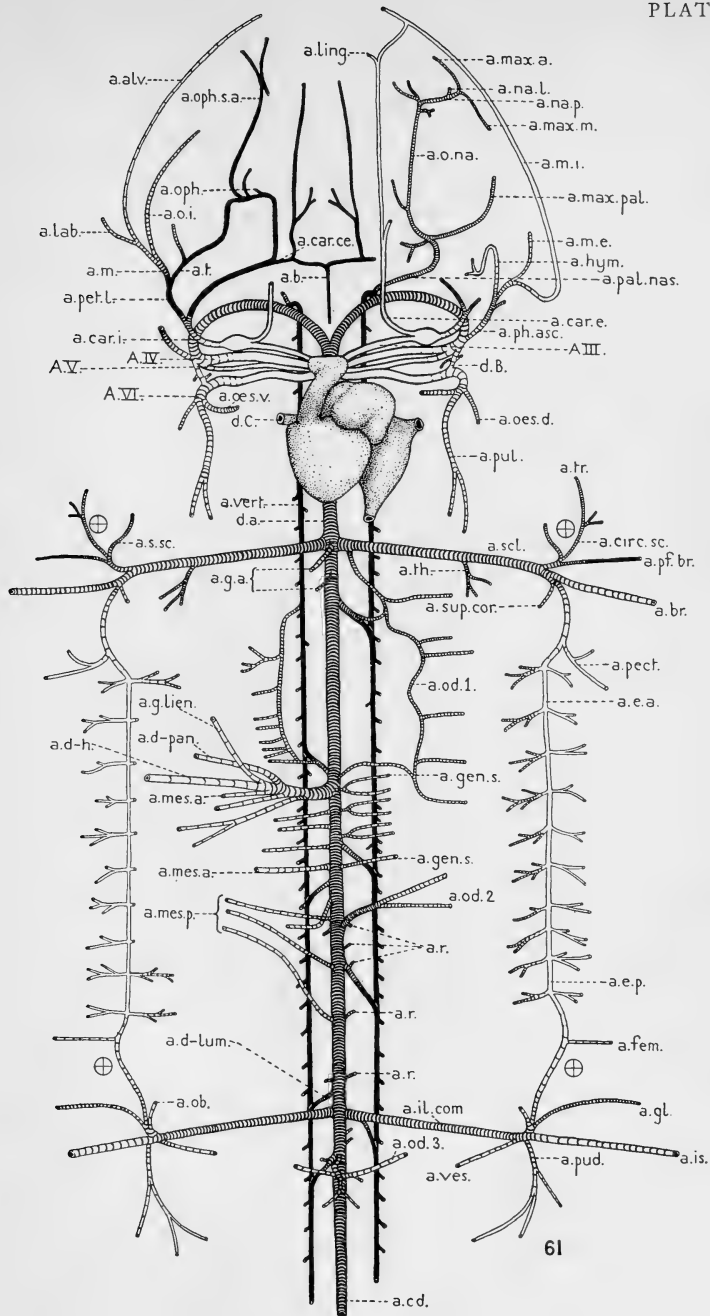
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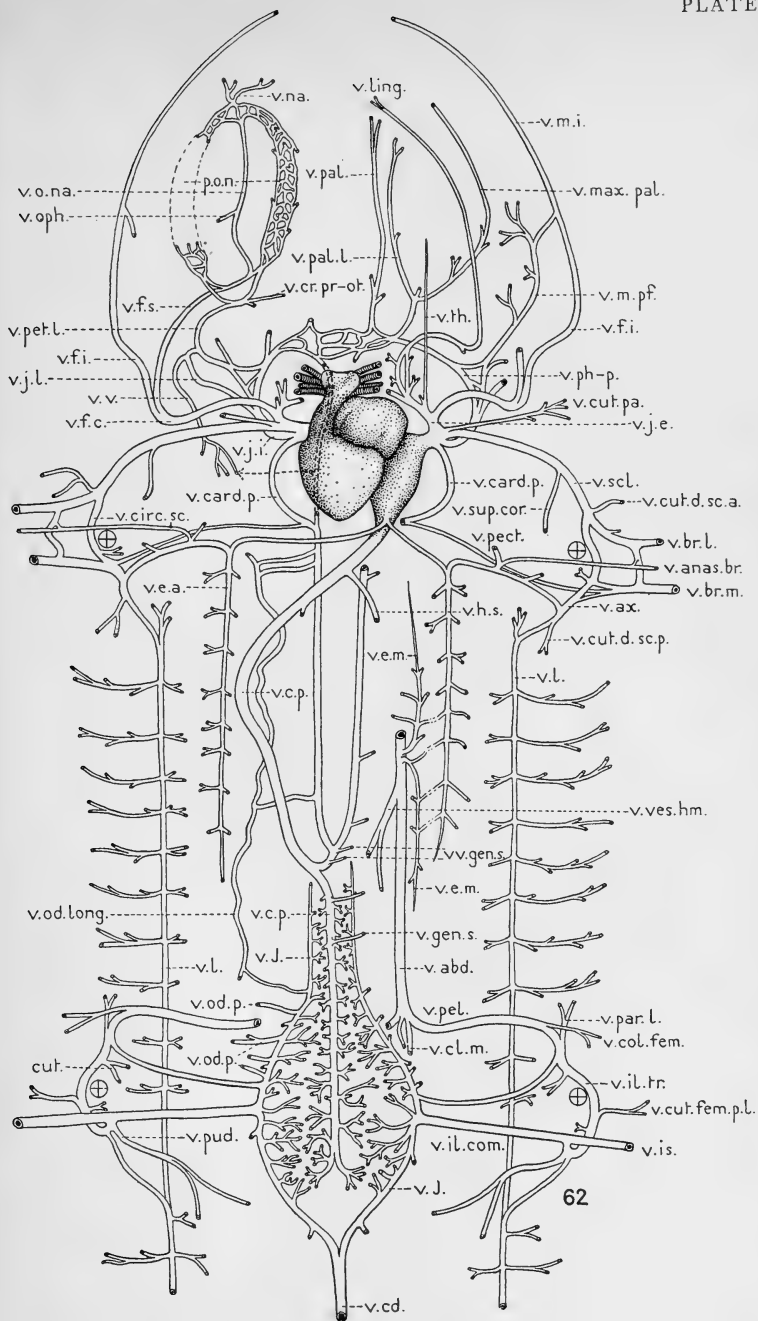




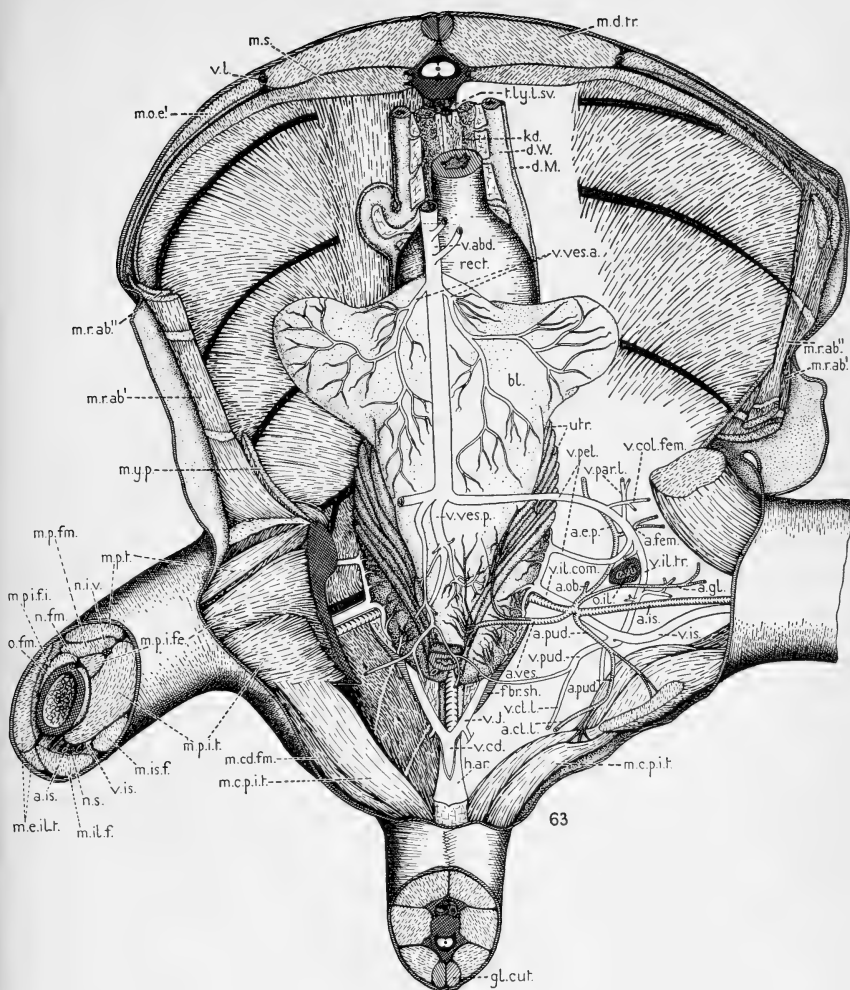


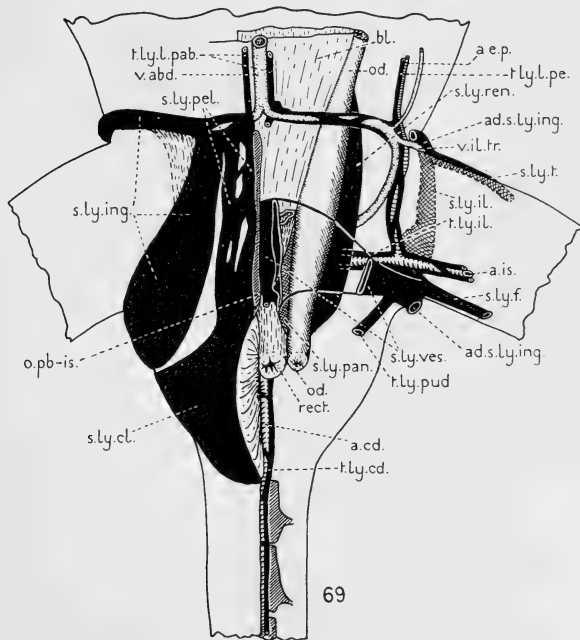
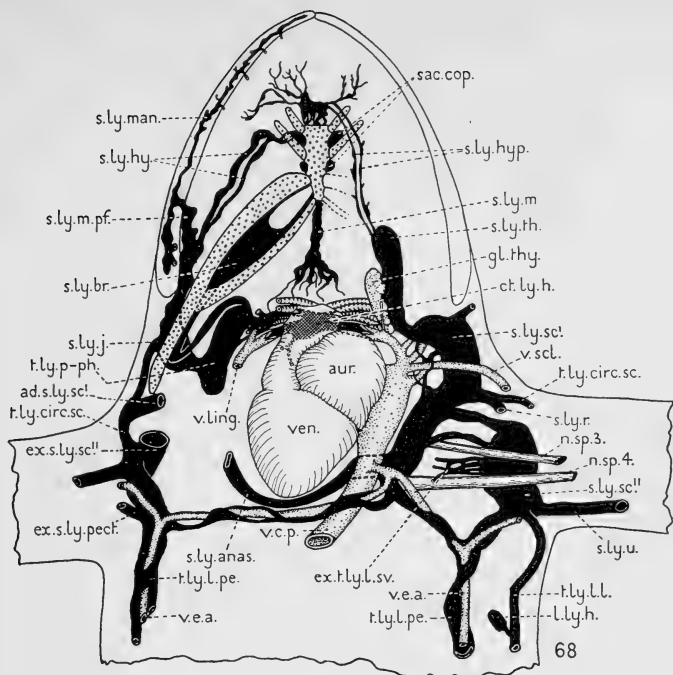


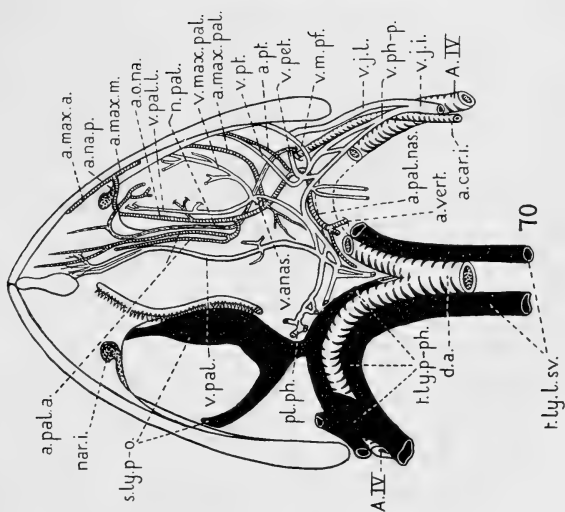
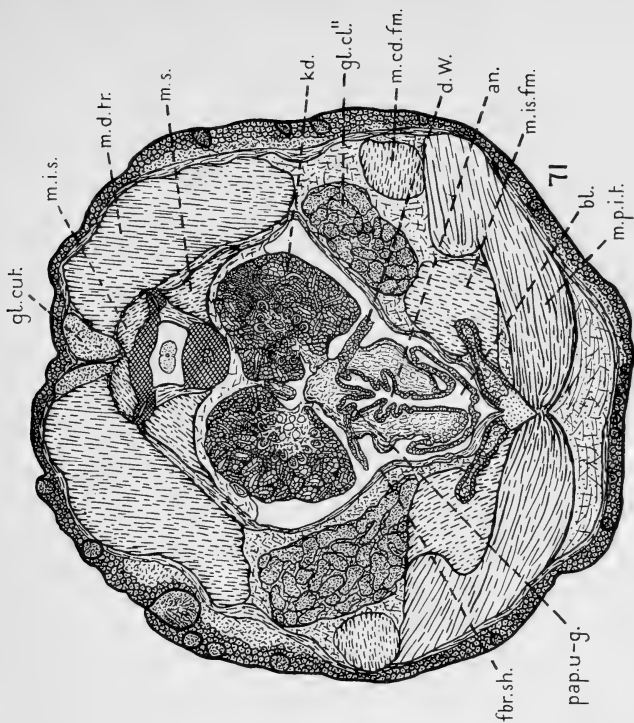


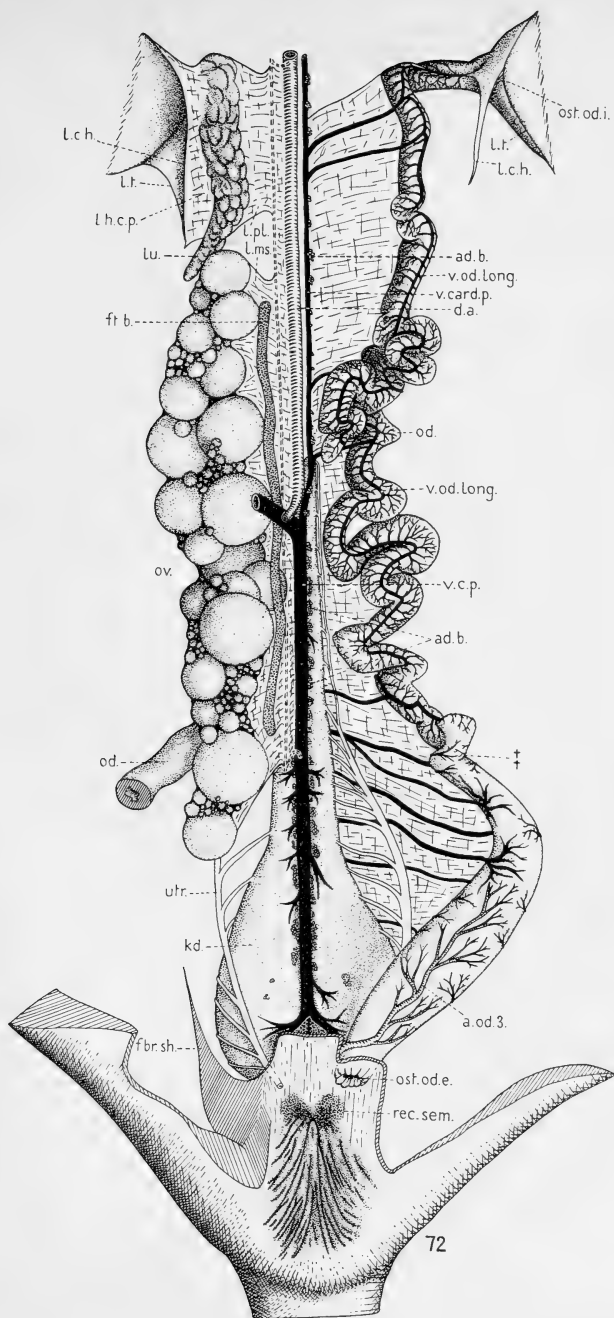


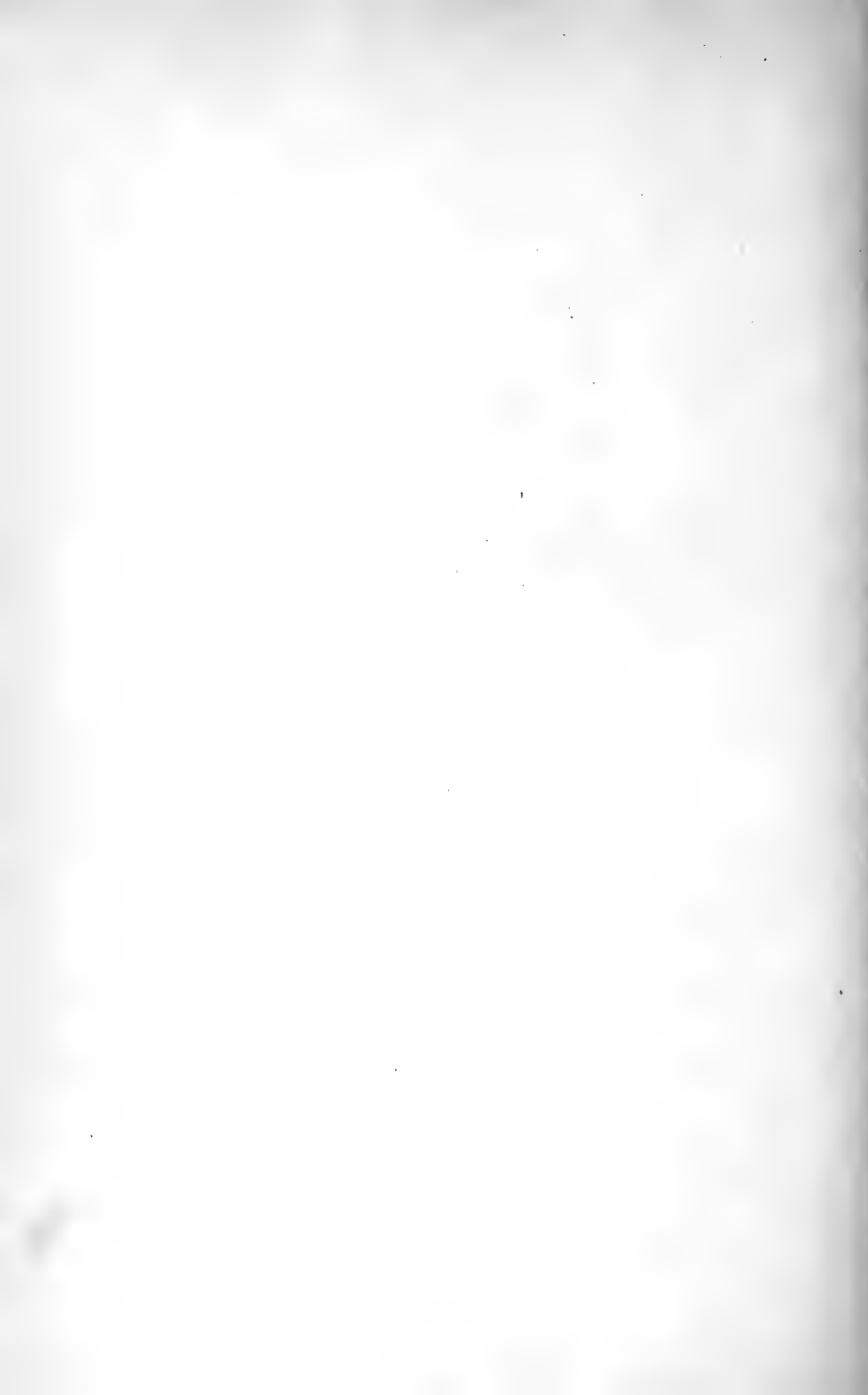


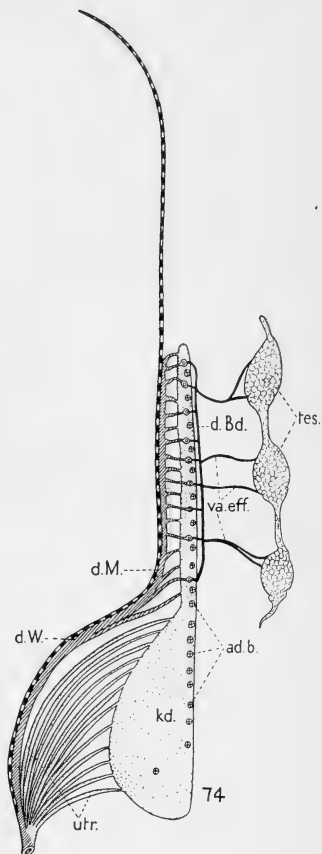
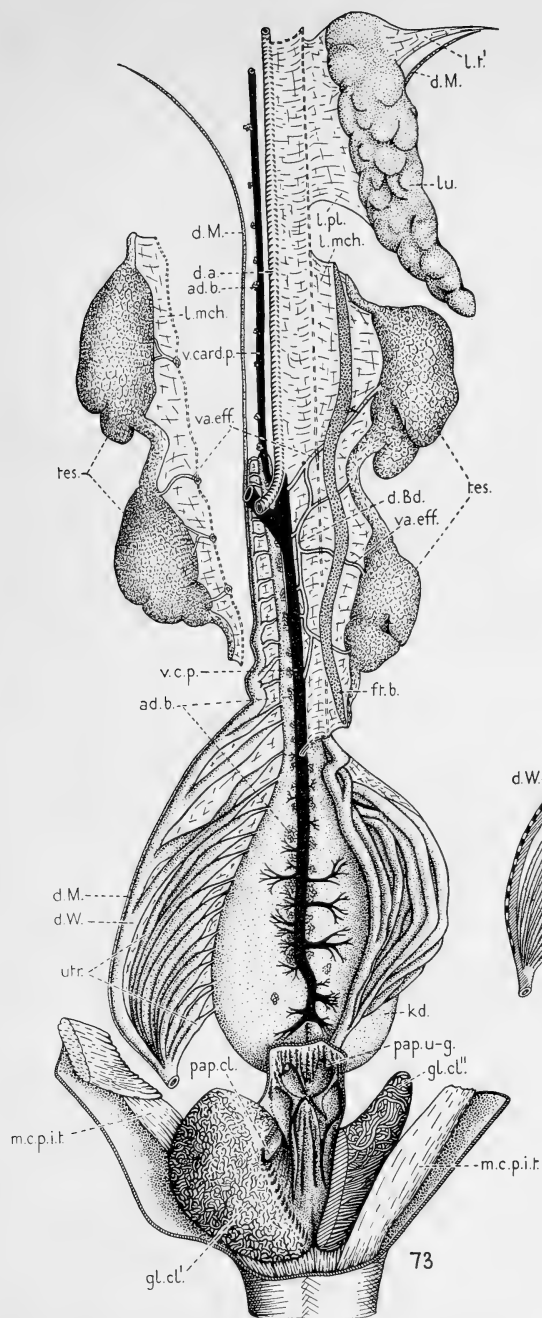


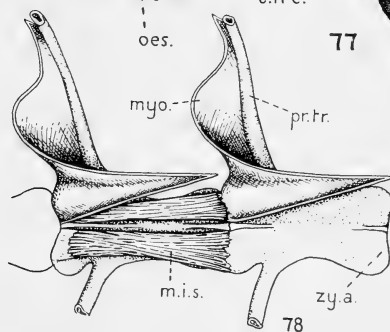
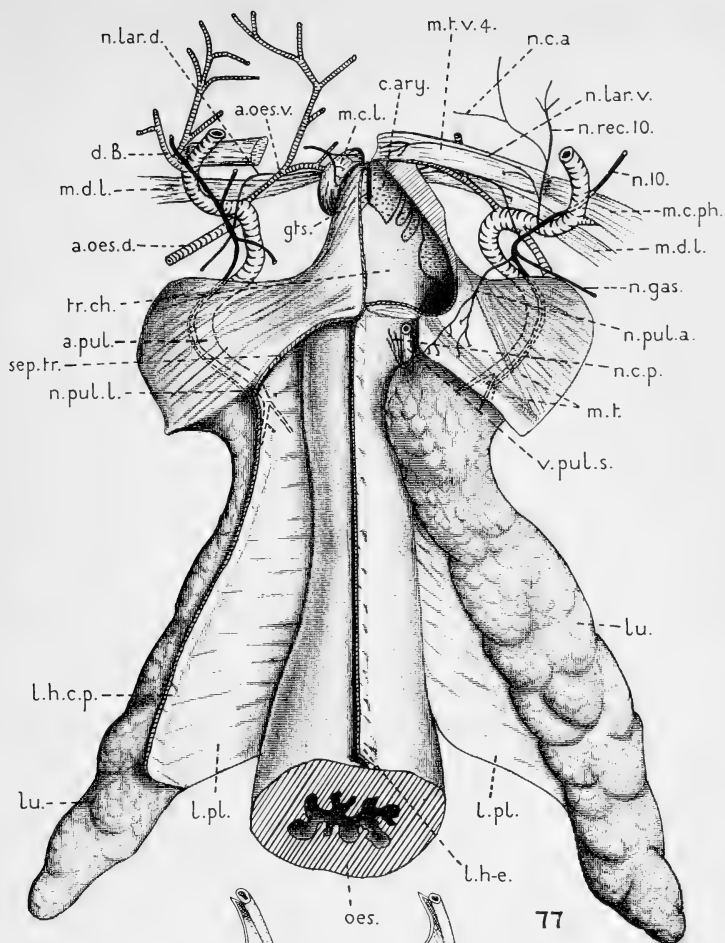


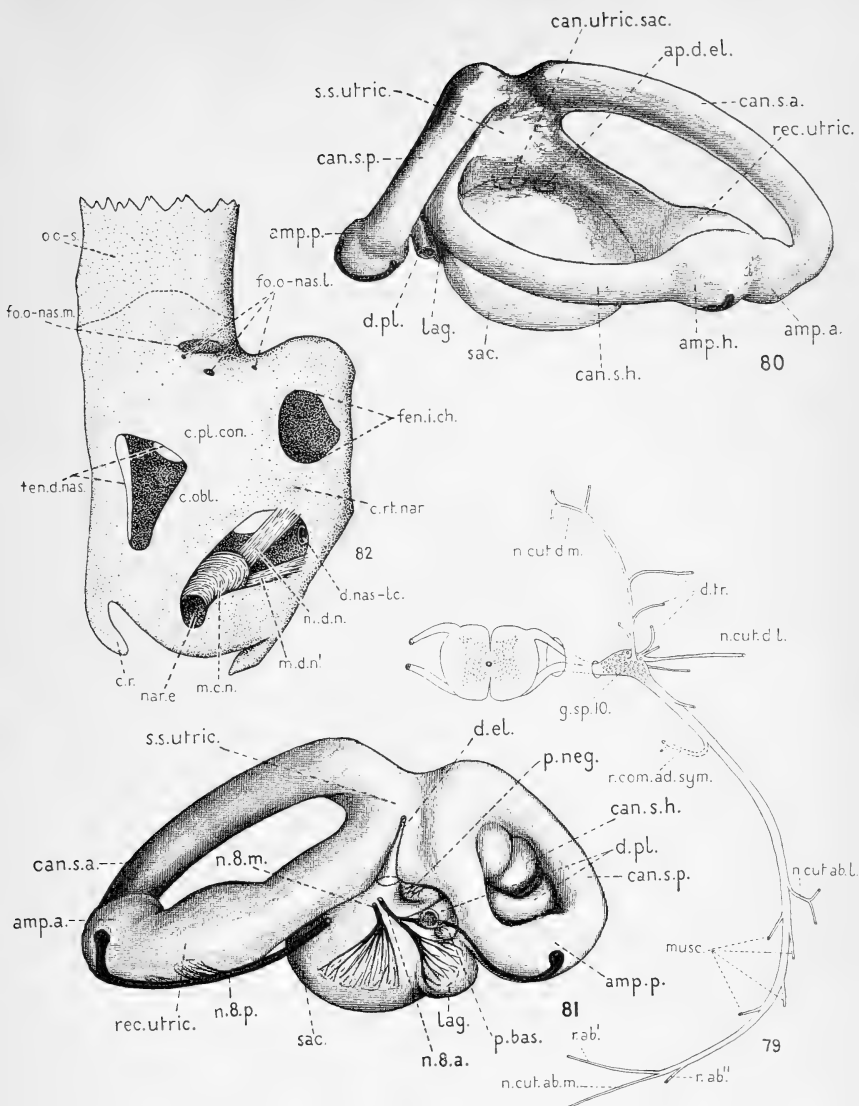












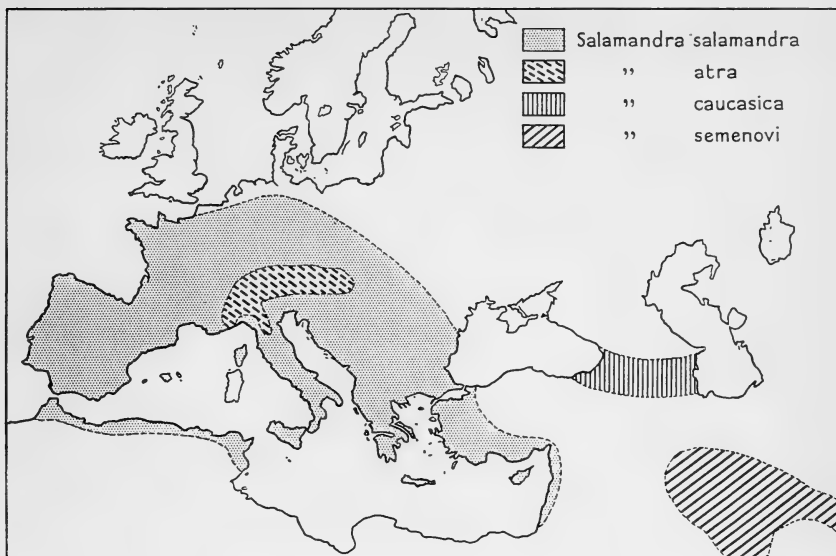


FIG. 83

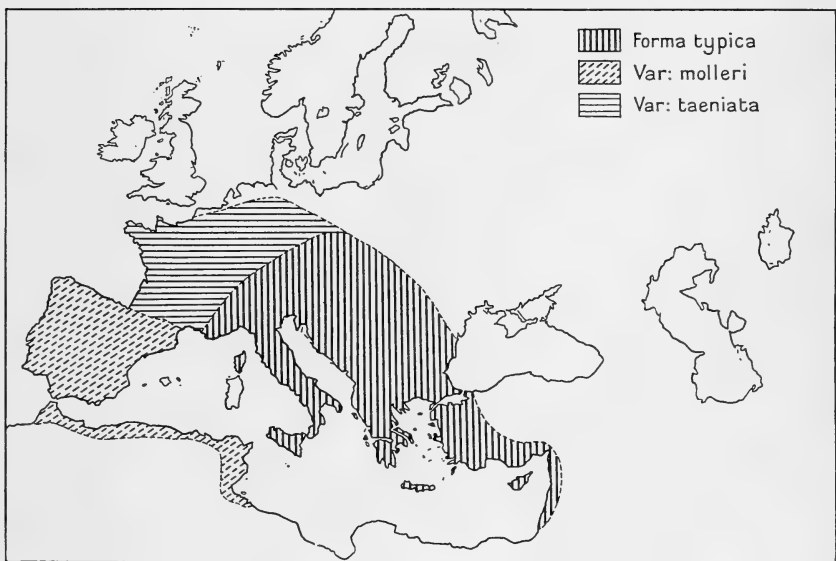


FIG. 84



2
1- 22
100, 182

